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THE RELATION OF THE EOCENE WILCOX FLORA TO SOME MODERN FLORAS [1]

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INTRODUCTION

One of the finest fossil floras known is found in deposits of Wilcox age in portions of Kentucky, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, and Texas (fig. 1). The first significant notice given the fossils of this flora was the paper by Lesquereux (1859). They have subsequently been mentioned by various authors, the most prolific of whom was Berry who described (1916) a majority of the species that are known. The same author in a subsequent paper (1930) added to and revised the list of Wilcox species and discussed at length their affinities.

In recent papers Brown (1939, 1940, 1944, 1946) has changed some of Berry's identifications and added to the list of Wilcox genera and species. In contrast to Berry (1916) who said "There is not a single strictly temperate type in the whole assemblage" of Wilcox fossils, Brown (1944, 1946) points out several temperate genera (*Betula, Comptonia, Fagus, Sassafras* and *Staphylea*) as components of this flora. Cain (1943), reviewing the Cretaceous and Tertiary fossil genera in the southeastern United States, found that 27 per cent are still extant in the flora of the Great Smokies, a distinctly temperate, and in part boreal, area.

However, no statistical comparisons between the known Wilcox genera and those from some of the modern floras have been published. Such comparisons are here attempted.

COMPARISON OF THE WILCOX FLORA WITH CERTAIN MODERN FLORAS

Using Small's Manual (1933) for a list of modern genera in the southeastern United States, it is found that there are still in this region 82 genera which were found in the Wilcox. Berry's list as amended by Brown includes 137 genera whose taxonomic position is known with more or less exactness. This suggests that 60 per cent of the known Wilcox genera still persist in the southeastern United States. Even if a considerable allowance is made for errors in the naming of the Wilcox fossils, the percentage is large enough to be significant.

The close relationship of certain genera in the southeastern United States with those in Asia has long been known and

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser., No. 126.

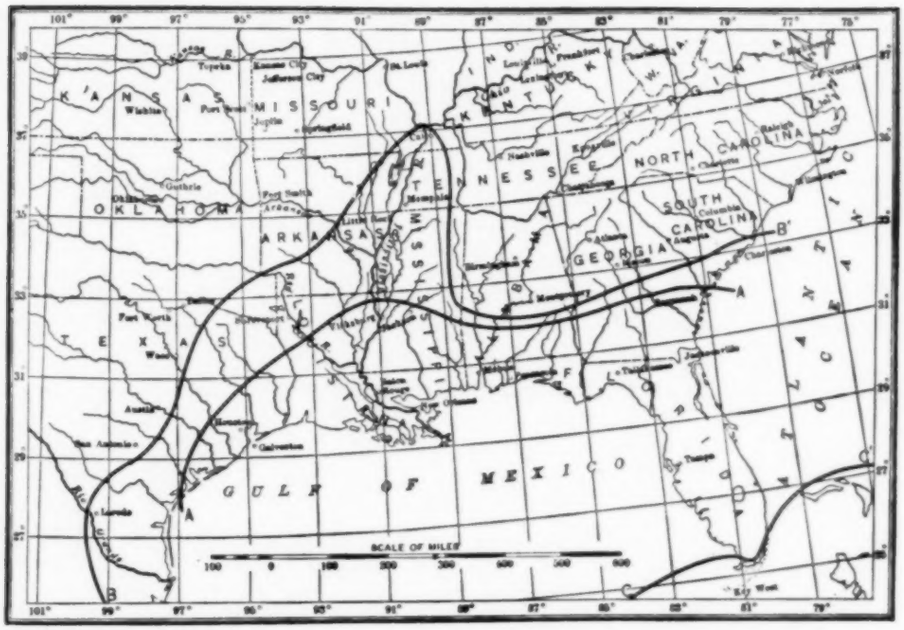

FIG. 1. Map showing (A–A') strand line at the beginning of Wilcox deposition, (B–B') the maximum extent of the Wilcox transgression, and (according to Berry) the northern limit (C–C') of the Wilcox flora under existing conditions. From Berry, U. S. Geological Survey Professional Paper 91, 1916.

was recently noted again by Cain (1943). With the assistance of Miss Ching-Yung Cheng [2] and using the publications of Forbes and Hemsley (1889–1905), Hu (1935), Lee (1935) and Sargent (1913–17), an attempt was made to compare the modern genera of central and eastern China with those of the Wilcox. Seventy-two of the 137 known Wilcox genera (53%) evidently still persist in that region. Considering the distance between the compared areas this seems rather remarkable.

There is another less remote area whose present vegetation contains a still higher percentage of the Wilcox genera. Miranda and Sharp (1950) in work on the vegetation of the eastern escarpments of the Central Mesa and of the Mesa de San Cristóbal in Mexico noted that a large number of Wilcox genera are still present in that Mexican flora. Including areas adjacent to the escarpments (altogether about one-third of the area covered by Small's 1933 manual), there is still extant in the flora of eastern Mexico 93 (68%) of the 137 designated Wilcox genera, a truly remarkable and highly significant correlation. The escarpment area alone has 35 per cent of these genera.

A list of the Wilcox genera still present in one or more of the following regions: 1. eastern United States, 2. central and eastern China, 3. eastern Mexico follows, and the floras in which they are currently indigenous are designated by symbols explained in the footnote.[3]

Acacia (2, 3*), *Acerates* (1, 3*), *Acorus* (2), *Anemia* (1*, 3), *Anona* (1*, 3), *Aralia* (1, 2, 3), *Aristolochia* (1, 2, 3*), *Artocarpus* (2), *Asimina* (1), *Asplenium* (1, 2, 3*), *Avicennia* (1, 2, 3), *Banara* (3), *Banisteria* (3*), *Berchemia* (1, 2, 3*), *Betula* (1, 2), *Buettneria* (2,

[2] Now a student at the Biological Laboratories, Harvard University; formerly at The University of Tennessee, and earlier at Chengtu, Szechuan. My sincere thanks are due her.

[3] 1—found in the southeastern U. S.; 1*—limited to peninsular and insular Florida; 2—found in central and eastern China; 3—found in eastern Mexico adjacent to the escarpments; 3*—found on the escarpments of the Central Mesa and Mesa de San Cristóbal.

3), *Bumelia* (1, 2, 3), *Caesalpinia* (1*, 2, 3), *Calyptranthes* (1*, 3), *Canavalia* (1*, 2, 3*), *Canna* (1*, 2, 3), *Capparis* (1*, 2, 3), *Carya* (1, 2, 3*), *Cassia* (1, 2, 3*), *Cedrela* (2, 3*), *Celastrus* (1, 2, 3*), *Ceratophyllum* (1, 2, 3*), *Cercidophyllum* (2), *Chamaedorea* (3*), *Cheilanthes* (1, 3*), *Chrysobalanus* (1*, 3), *Chrysophyllum* (1*, 2, 3), *Cinnamomum* (2), *Citharexylon* (1*, 3*), *Cladrastis* (1, 2), *Coccolobis* (1*, 3), *Combretum* (2, 3), *Comptonia* (1), *Conocarpus* (1*, 3), *Cordia* (1*, 2, 3*), *Cryptocarya* (2), *Dalbergia* (1*, 2, 3), *Diospyros* (1, 2, 3), *Dodonaea* (1*, 3), *Dryopteris* (1, 2, 3*), *Drypetes* (1*, 3*), *Engelhardtia* (2, 3*), *Equisetum* (1, 2, 3*), *Eugenia* (1*, 2, 3*), *Euonymus* (1, 2, 3*), *Exostema* (3), *Fagara* (1*, 2, 3), *Fagus* (1, 2, 3*), *Ficus* (1*, 2, 3*), *Fraxinus* (1, 2, 3*), *Gleditsia* (1, 2), *Glyptostrobus* (2), *Guettarda* (1*, 2, 3), *Hiraea* (3*), *Hymenaea* (3), *Icacorea* (1*, 3), *Ilex* (1, 2, 3*), *Inga* (3*), *Juglans* (1, 2, 3*), *Laguncularia* (1*, 3), *Liquidambar* (1, 2, 3*), *Lygodium* (1, 3*), *Magnolia* (1, 2, 3*), *Manihot* (3), *Maytenus* (1*, 3), *Metopium* (1*, 3), *Mimusops* (1*), *Myrica* (1, 2, 3*), *Nectandra* (1*, 3*), *Negundo* (1, 2, 3*), *Nelumbo* (1, 2), *Nyssa* (1, 2, 3*), *Oreodaphne* (2, 3*), *Oreopanax* (3), *Osmanthus* (1, 2, 3), *Ouratea* (3), *Paliuris* (2), *Parkinsonia* (1*, 3), *Persea* (1, 3*), *Pisonia* (1*, 2, 3), *Pistia* (1*, 2, 3), *Pithecolobium* (1*, 2, 3*), *Platanus* (1, 3*), *Potomageton* (1, 2, 3*), *Prunus* (1, 2, 3*), *Pseudolmedia* (3), *Psychotria* (1*, 2, 3*), *Ptelea* (1, 3*), *Pteris* (1, 2, 3*), *Rhamnus* (1, 2, 3*), *Salvinia* (1, 3), *Sapindus* (1, 2, 3), *Sassafras* (1, 2), *Schefflera* (2), *Sideroxylon* (1*, 2, 3), *Simaruba* (1*, 3), *Smilax* (1, 2, 3*), *Sophora* (1, 2, 3), *Sparganium* (1), *Staphylea* (1, 2, 3*), *Sterculia* (2, 3), *Taxodium* (1, 3*), *Terminalia* (2, 3), *Trapa* (2), *Zamia* (1, 3), *Zizyphus* (2, 3), *Zygophyllum* (2).

Discussion

Reference to the above list will indicate that 48 of the Wilcox genera (35%) are present in the flora of the eastern escarpments in Mexico. Forty-five other genera (33%) are growing in neighboring areas, chiefly the coastal plain. Evidently the flora of eastern Mexico in and around the escarpment areas is more closely related generically to the plants of Wilcox time than are those either of the southeastern United States or of central and eastern China, if the modern generic composition is a reliable criterion.

Two of the more important elements of this Mexican flora are the oaks and pines, which seem to be lacking or poorly represented in the Wilcox flora. This discrepancy might be the result of a failure in the preservation of the plant materials. It is not improbable, however, that they were (if not lacking) less abundant in the Wilcox than in the modern Mexican vegetation. Perhaps pollen analyses of the Wilcox clays would change the picture.

It is possible that some of the fossils assigned to *Dryophyllum* by Berry (1930) are more closely related to some of the modern Mexican oaks whose leaves they rather closely match. The resemblance of *Parrotia cuneata* (Newberry) Berry (1916) to the leaves of some of these oaks is too close to be ignored. That the oak genus had already evolved is confirmed by Dorf (1942) who found it present in the Upper Cretaceous floras of the Rocky Mountain region.

The earliest fossil pine to be found in the eastern United States seem to be that in the Mt. Vernon (Older Potomac, Lower Cretaceous) series, which was described by Ward (1905) and listed as Mesozoic. There is still no evidence that any pine was a part of the flora in the region adjoining the basin of Wilcox deposition.

These discrepancies must be taken into consideration in any comparison of the Wilcox climate with the modern climate of eastern Mexico. There still remain, however, a sufficient number of important genera such as *Liquidambar, Oreopanax* and *Myrica*, common to the two floras to

suggest that the climate of the Wilcox was not too unlike that of eastern Mexico at the present time. Chaney (1938, p. 383) notes that it places too great a burden upon the laws of chance to suggest that a large number of plants have changed their climatic requirements, all in the same direction, since early Tertiary time.

Berry (1930) considered the Wilcox flora as essentially subtropical, if not tropical (fig. 1). It must be admitted that most of the Wilcox genera as represented in the modern floras seemingly cannot withstand freezing temperatures. There are some, however, that grow chiefly in regions with a distinctly temperate climate. Those which are to be found in (and in some cases restricted to) such areas, even in Mexico, include such genera as *Carya, Engelhardtia, Fagus, Juglans, Liquidambar, Magnolia, Myrica, Nyssa, Ptelea.*

Chaney (1940) indicated that plant materials may not be moved far before being deposited in sediments prior to fossilization. If this is true, in view of the Wilcox genera which today are restricted to or occur chiefly in temperate climates, the temperatures of the region bordering the Wilcox basins must have been somewhat lower than would be postulated for a strictly tropical flora. If the plant materials were carried some distance, the pre-Ozarkian and pre-Cumberland highlands could perhaps furnish the necessary environments for the less tropical Wilcox genera. It may be suggested that there were one or more climatic shifts during the Wilcox, but such changes cannot account for fossils of such diverse genera as are listed by Berry (1916) from single locations.

There is another alternative which might be suggested.[4] Could it be that these genera in the Wilcox inherently had a greater amplitude of ecological tolerances than most of them seem to have today? A few of them still exhibit great tolerances. For instance, *Liquidambar* in the Americas is considered as a single species, yet I have seen it growing at 1,400 feet elevation in the wet, tropical forest, among palms, figs and other tropical genera on the headwaters of the Coatzocoalcos River in Oaxaca, Mexico, and also at the considerably higher latitude of southern Ohio. *Nyssa* in the Americas has three or four (perhaps fewer) closely related species which range from New England to the Gulf coast and at least one of them, *N. sylvatica,* is found again in Puebla and Chiapas, Mexico. It is possible that segregation to less general genetic types and extinction of some of them have left modern genera with less ecological amplitude than they had in Wilcox times. It is also possible that the present geographic distribution of some modern representatives of Wilcox genera does not give a true picture of their ecological amplitude as, for example, in postglacial times they may not have migrated to their ultimate boundaries.

It appears to me either that a greater genetic variability at the generic level existed in the Wilcox flora, or that plant materials were transporated quite some distance prior to fossilization, or that a large number of plant genera have changed their climatic requirements all in the same direction since early Tertiary times. The first alternative seems most plausible to me and I suggest that the comparisons between the known Wilcox vegetation and modern floras merits further attention by the evolutionists.

Summary

Eighty-two (60%) of the 137 Eocene Wilcox genera known with some certainty are present in the modern flora of the southeastern United States; seventy-two genera (53%) are in the modern flora of central and eastern China; ninety-three genera (68%) are extant in the

[4] After this manuscript was submitted for publication my attention was called to the work of MacGinitie (1941). This excellent treatise should be consulted (especially the section: "Ecological Considerations," pp. 62–70) by all interested in this problem.

vegetation now on or near the escarpments of eastern Mexico.

This high correlation with the vegetation of eastern Mexico may suggest that the Wilcox climate was similar to that of the Mexican escarpment region, which shows a mixture of temperature and tropical conditions.

If some of the plant materials were not transported in Wilcox time from the pre-Ozarkian and pre-Cumberland highlands, it is possible that such genera as *Fagus, Betula* and *Sassafras,* today considered as temperate forms, had a greater ecologic amplitude then than now.

Another less probable alternative is that a large number of genera have changed their ecological requirements all in the same direction since Wilcox (Lower Eocene) times.

Acknowledgments

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THE BRAINS OF THE ODONTOGNATHAE

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THE "BRAIN CASTS" AND THEIR MEANING

"Fossil brains" are now known in such large numbers that they are no more merely contributions to the anatomy of a few extinct vertebrates; some of them have disclosed stages of brain evolution in several ancestral series. Such specimens are not really brains; fossilized brain matter has not been found. The vanished brain, however, had moulded the walls of the cranial cavity, so that its form can be reproduced in endocranial casts of fossil skulls. While in the majority of lower vertebrates the endocranial cast is not an exact replica of the brain because the endocranial cavity contains relatively wide circum-cerebral spaces, in most mammals and in all birds the endocranium is a tightly fitting bony capsule of the brain and its cast therefore is, to all intents and purposes of macroscopic study, a brain.

Most general types of modern birds had evolved by the beginning of the Cenozoic era, almost 75 million years ago. Avian fossils from the preceding Mesozoic era have been discovered only in geographically widely separate spots of the earth, in strata laid down at widely separate times of earth history. Those from the Upper Jurassic of Eichstätt, Germany, and the Upper Cretaceous of the Smoky Hill River region of Kansas—about 130 and 80 million years old, respectively—include material suitable for paleoneurological study.

For 70 years we have had a definite conception of the brains of *Hesperornis regalis* and *Ichthyornis victor*. "Two brain casts" were described and figured by Marsh (1880, pp. 8–10 and 121–125, figs. 1 and 29) in his monograph on the toothed birds of Kansas, "Odontornithes," and this tome "is still a classic and was and remains one of the best paleornithological works" [1] in the opinion of the eminent paleornithologist, Lambrecht (1933, p. 246). The descriptions and figures were reprinted in Marsh's 1883 report (pp. 55–57 and 71, figs. 7 and 19). They introduced to the world two endocranial casts representing brains in an extremely interesting evolutionary stage. "The brain of *Hesperornis* was quite small, and more reptilian in type than in any adult bird hitherto examined" (p. 8). "The brain of *Ichthyornis* was remarkably small, and in its main features, strongly reptilian" (p. 121).

Whereas reptilian features of the two ancient bird brains and their similarity are matters of great importance to the present generation of scientists, a relatively small brain can no longer be regarded as a character of either neurological or evolutionary significance. Marsh believed that through the ages "There was a gradual increase in the size of the brain" within the classes Reptilia, Aves and, particularly, Mammalia (pp. 10–11). In the two Odontognathae "The diminutive elongated brain, also, points back to the reptiles" (p. 179). Even d'Arcy Thompson, who found in *Hesperornis* osteological "resemblances almost amounting to identity with the existing Colymbi," regarded as equally striking "the two marked peculiarities of the teeth and the undersized brain" (1890, p. 14). Actually, the length ratio of brain to skull happens to be the same (1 : 3.7) in *Hesperornis* and the Recent *Colymbus* (*Gavia*) of Marsh's figures (figs. 1, 2), and is far smaller in longer-beaked birds (1 : 7.9 and 1 : 8.5 in two *Pelecanus* of the Museum of Comp. Zoöl. bird collection). There are small birds whose brains are, relative to body volume, larger than human brains and about one hundred times as large as ostrich brains. Such dissimilarities in the brain to

[1] I have translated foreign language quotations. Quotations cited without naming an author are from Marsh 1880.

body ratio exist also in the class from which birds evolved, the Reptilia—e.g. between small and giant snakes, forms similarly efficient and on similar levels of evolution. Similarly, the brain cavity is small in *Hesperornis*, of whose great body size Marsh has given such a peculiarly impressive description by writing (p. 112) "that the skeleton, if extended, would measure about 6 feet (1.8 m.) from the point of the bill to the end of the toes." According to Marsh's figures, the brain cavity is 64 mm. long in *Hesperornis* and almost half that, 31 mm., in *Ichthyornis*, while skull lengths are 257 mm. and 100 mm., respectively. The differences in body size can be illustrated by Marsh's length measurements of four tibiae of *Hesperornis*: 320–335 mm. (p. 92) and two of *Ichthyornis*: 57 mm. (p. 173). Thus according to Marsh's own figures the pigeon-sized *Ichthyornis* had, relatively, a far larger brain than the large *Hesperornis*. *Ichthyornis*, however, was in many ways the more primitive of the two genera.

The reptilian type of brain Marsh had in mind is that of the living, creeping forms. These brains presumably have remained close to a general type of primitive reptilian brain from which has gradually evolved the type of brain, distinctly different, which is highly characteristic of all Recent birds. Marsh's example (fig. 3) belongs to the order Crocodilia, a group whose brains (fig. 4) are in several features more advanced than are the other extant reptilian brains (e.g., fig. 6), but this does not necessarily exclude them from the morphological series culminating in the bird brain. The Recent Crocodilia are the only survivors of the reptilian subclass Archosauria from which evolved the class Aves; the progressive features of crocodilian brains are advances in an evolutionary direction similar to that which has lead to the bird brain. The differences of the bird brain from the reptilian are, of course, connected with the higher evolutionary level which the avian organism has achieved. They are essentially a matter of cell and fiber anatomy to which paleoneurology has no direct access. At the same time, striking peculiarities in gross morphology are also related to the special avian mode of life. In contrast to the condition in the ancestral reptiles, the head organs in birds are closely packed in a tightly-fitting skull; sight and equilibrium are the dominating senses, while the role of smell is insignificant. The relation of external morphology with internal structure and function is clearly seen in the brain-eyes complex in the birds themselves, and it is further proven by the fact that an "avian" shape of brain was also developed in both branches of the extinct order of flying reptiles, the Pterosauria (Edinger, 1928, 1941; see fig. 7).

In birds (figs. 5, 8) the cerebrum is a far larger portion of the brain than in reptiles (always excluding pterosaurs). In striking contrast to reptilian cerebral hemispheres, those of birds are very broad, and have at least one sulcus. They rise along the posterior walls of the large orbits, above which lie the short olfactory bulbs. The avian cerebellum is lobulated and is developed to such size that it is usually in contact with the occipital surface of the cerebrum. The cerebrum, 'tweenbrain, midbrain, and cerebellum of the primitive reptilian brain are serially arranged in a wide brain cavity, but in birds the optic lobes of the midbrain roof are displaced to a lateral position and protrude into special concavities of the lateral brain case walls. In dorsal views of bird brains only the outer margins of the optic lobes are visible. These lateral lobes are overlapped by the cerebrum and by the cerebellum, which also overlaps practically the whole medulla oblongata. The latter is a smaller portion of the brain than in reptiles.

According to Marsh's description of the *Hesperornis* and *Ichthyornis* brains, these avian characteristics had not been achieved in either genus. According to his figures (our figs. 1 and 10), the optic lobes were in the avian position, but they were largely exposed dorsally. The Cretaceous bird brains represented according to him an evolutionary level intermediate between that of extant reptiles and extant birds.

Thus it appeared that here were two birds so different that they represent two orders—of equal antiquity however and both retaining such ancestral features

as teeth, non-united lower jaws, and a reptilian type of brain. According to Marsh, the brain of *Ichthyornis* "In form and proportions . . . resembled the brain of *Hesperornis* more nearly than that of any other bird" (p. 121).

The resemblance between the two ancient bird brains consisted in their primitive character, distinguishing them both from all Recent bird brains. This condition which Marsh had described came to be a phenomenon of great importance in present-day paleoneurology. We now know that some early Tertiary mammals with variously specialized skeletons had brains of similarly primitive proportions (Edinger, 1948, pp. 27–33; Edinger, 1950). A partial endocast of *Archaeopteryx* suggested that in the most ancient feathered animal, 130 million years ago, the brain was of reptilian type (Edinger, 1926). In the Upper Cretaceous, some 50 million years later, bird skeletons were modern except in some isolated features; but it seemed that the brain still had not become that kind of organ which in the Cenozoic is part of every avian organism.

A brain similarly primitive in *Hesperornis* and *Ichthyornis* seemed another sign of brain evolution proceeding independently of body specialization. *Hesperornis* was a large and specialized swimming form, but *Ichthyornis* was a small and "normal" flying bird. It was more primitive than *Hesperornis* also in not having developed the avian type of vertebral articulation.

Thus the significance of Marsh's material reached far beyond the field of paleontology. The similarity of the brain in the two different ancient birds was so impressive that it invited generalization. Marsh's descriptions have been quoted and discussed and his figures reproduced in innumerable papers, books and handbooks of various kinds—usually as representing *the* brain of Cretaceous, sometimes as *the* brain of fossil birds.

To Heilmann, for example, Marsh's specimens appeared so important that his treatise on the origin of birds (1927) not only contains Marsh's figures of the endocranial casts in the chapter on fossil birds, but in the chapter on bird anatomy the two Cretaceous brains are shown in improved drawings. The dorsal brain views of Heilmann's figure 88 also include the extant alligator (No. 4) and show *Hesperornis* (6) and *Ichthyornis* (7) flanked by the Jurassic pterosaur *Scaphognathus* (5) and the extant bird *Dafila*. Heilmann comments (p. 108), that "The series of brains in fig. 88, 4–8, plainly shows the transitional stages from the reptilian to the bird's brain; in fact, there is a much greater break between the brains of the Cretaceous birds and that of the recent birds, than between the brains of the reptile and the Cretaceous birds."

The two Cretaceous brains were the only avian evidence at the following incident. At the 1885 meeting of the British Association for the Advancement of Science, Marsh read a paper on his theory of gradual increase of the brain size in mammals during the Tertiary period. He added that there was "now evidence that the same general law of brain growth holds good for birds and reptiles from the Jurassic to the present time." The speaker was congratulated by one of the greatest of zoölogists; "Nature" reported that "Prof. Flower said it was satisfactory to find a case where the facts worked out coincided with previously-formed theories, because that was not always the case, and sometimes the facts or the theories had to go to the wall."

Quotations from recent papers will show how lasting can be the effect produced by the publication, as momentous discoveries, of specimens not re-examined in 70 years. De Lapparent and Augier (1947, p. 729) state that "The Cretaceous birds, whose innumerable remains have been discovered in America in the 1870's, all had teeth and a brain still recalling much that of the reptiles: olfactory bulbs strongly developed, cerebral hemispheres smaller, and bigeminal lobes less projecting than in a recent bird and even in the pterosaurs." Like so many others, the present author has used the data reported by Marsh as a base for study. My redescription of the two endocasts (1929, pp. 143–144) relied on Marsh's figures. Recently, when contrasting the diversified evolution of mammals with avian evolution, I wrote that one "could have constructed the *Hesperornis* brain as a hypothetical intermediate between the oldest and the extant birds brains" (1949, p. 11).

It is the purpose of the present paper to show that both the *Hesperornis* and *Ichthyornis* "brains" are hypothetical reconstructions. No "theories had to go to the wall" (Flower) on account of these

"brain casts," because they do not exist and never have existed as actual specimens.

In the course of a survey of fossil brains in American collections [2] I visited the Peabody Museum of Yale University (YPM) in December 1949. Dr. J. T. Gregory had assembled all endocranial casts from Marsh's and later Yale collections. He had not found the *Hesperornis* and *Ichthyornis* endocasts Marsh had described and figured. Our investigation of the entire skull material of Cretaceous birds in the Yale collections convinced us that there is no cranium present from which such casts could have been taken.

After inquiries at other museums [3] known to have acquired "complete skeletons" of Cretaceous birds, it appears that no crania of either *Hesperornis* or *Ichthyornis* are known to exist except those discovered during Marsh's expeditions. A skull of *Hargeria* (Marsh's *Hesperornis gracilis*) is in the Museum of Natural History of the University of Kansas; in this specimen "portions of . . . ribs had become crushed into and intimately associated with the cranium" (Lucas, 1903, p. 545). A recent letter from Dr. R. W. Wilson confirms the fact that this cranium cannot be used for endocasting. We must realize that not enough material has been found for us to known the odontognathous stage of bird evolution as fully as Marsh's monograph made us believe we did. The descriptions given below show that although the material available is poor a revision of the specimens pertinent to paleoneurology leads to results contradicting Marsh's main conclusions which have hitherto been unchallenged supports of certain vague ideas concerning vertebrate evolution.

[2] Aided by a grant from the Milton Fund of Harvard University.

[3] United States National Museum, American Museum of Natural History, British Museum (Natural History).

HESPERORNIS REGALIS

The "skulls"

Marsh reported that *Hesperornis* is represented by remains as complete as any fossil skeleton yet discovered, and that he had specimens of about 50 individuals (p. 5). Lambrecht, consequently, was under the impression that Marsh had endocranial casts made of several specimens (1933, p. 251). Marsh's list of measurements, however, rightly identifies only two by number (pp. 11–12). The holotype skull, YPM 1206, is "the very perfect specimen" which in figure 1 supposedly "is represented with the outline of the brain-cavity in position. The skull of the Loon is added in figure 2, *also* with a *cast of the brain* in natural position" (p. 8; italics mine). The second "Skull (*Hesperornis regalis*, No. 1207)" consists of a quadrate bone and the occiput.

Contrary to figure 1, and to the figures on Marsh's plate 1 and its legend, the holotype skull consists of a number of fragments scattered over a slab. Marsh showed as connected the 130 mm.-long beak portion and the 98 mm.-long cranium-orbits portion. These presumably were close to each other, but they now lie 100 mm. apart. Thus we really cannot know exactly how long this skull was.

The cranio-orbital fragment is so prepared that it can be lifted from the slab and studied from all sides. The cranium is dorso-ventrally flattened and much broken and there cannot be any doubt as to its being in the condition in which it was found and prepared. No endocranial cast can ever have been taken from this specimen. The posterior end of the endocranial matrix is seen in the foramen magnum, but the anterior end of the brain case cannot be traced in this skull. It follows that, like the length of the skull, the length of the brain is not known. Figure 1, which we believed to show a complete *Hesperornis regalis* skull with its endocranial cast, actually represents a reconstructed skull and Marsh's idea of a *Hesperornis* brain.

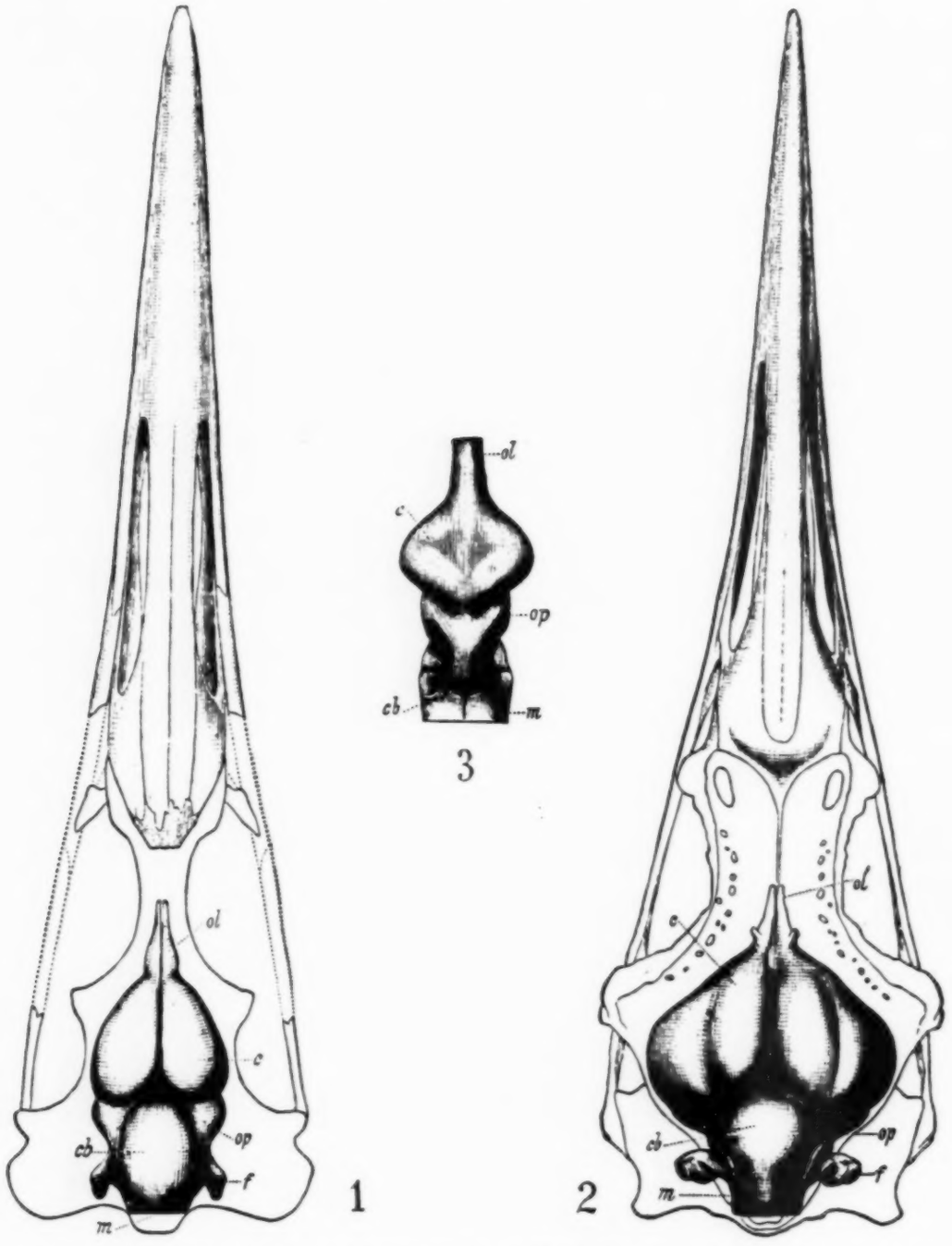


FIG. 1. "Outline of skull and brain-cavity of *Hesperornis regalis* Marsh; seen from above" (× 3/5). FIG. 2. Same of *Colymbus* (× 1). FIG. 3. Endocranial cast of young alligator (× 1). From Marsh, 1880.

The holotype and the forebrain

Whereas the specimen does not directly reveal any neurological data, it shows that the brain of *Hesperornis* cannot have had the proportions described by Marsh. Most important from an evolutionary viewpoint is the cerebrum, represented as "of very moderate size, much smaller, proportionably, than in any existing birds, and strongly resembling the corresponding part in some reptiles. The two lobes were narrow, and subovate in outline." It is quite true that no Recent bird has a cerebrum so short that its length ratio to the whole brain is 1 : 2.6 (fig. 1); but the specimen contains no feature what-

ever indicating the supposed shortness of the cerebrum. It is also true that no Recent bird has narrow cerebral hemispheres; but the specimen reveals that the cerebrum of *Hesperornis* was not as slender as it has been reconstructed. We mentioned above the close proximity of brain and eyes in birds. Its intimate relation to the eyes is graphically illustrated by Hofer's describing the orbit of most birds as "almost completely closed posteriorly by the cerebral capsule" (1945, p. 13). Further, in the economically-built bird body, circum-cerebral spaces are reduced to a minimum. Brain and eyes are separated only by a thin sheet of bone. Through this configuration, the maximum width of the bird cerebrum is situated in, or extends forward to, the transverse plane directly behind the eyes. In both a longitudinally halved *Colymbus* skull (MCZ Bird Dept. 772) and a transversely sectioned *Colymbus* skull (YPM 2254), the greatest lateral expansion of the cerebral chamber lies exactly under the postero-medial edge of the postorbital process. In the large *Pelecanus* (MCZ 1448) and the little *Sterna* (YPM 2195), the hemispheres bulged into the roots of the postorbital processes, and maximum cerebral width was in the middle of the inner border of the process.

When one studies Marsh's figure of the *Hesperornis* skull and brain, remembering that the greatest transverse extent of the avian cerebral capsule is related to, and lies close behind the orbits, one realizes that this figure ascribes to *Hesperornis* a cerebro-cranial relation different from that in all other birds, including *Archaeopteryx*. How could we ever believe that a bird cerebrum had its greatest width in the narrowest region of the cranium? The figure shows maximum cerebral breadth in the transverse plane of greatest cranial constriction between the temporal fossae! The figure at the same time does show the cerebral capsule widening anterad from this plane—which is indeed the condition in the specimen. Our having been taken in by Marsh's figure is, I feel, particularly embarrassing because in the very same monograph Marsh, reconstructing a left side view of the *Hesperornis* skull (pl. XX—based on the same specimen as his fig. 1), has shown that he himself assumed the normal condition. In the reconstruction, *Hesperornis* has the typically avian brain-moulded cerebral capsule, with its widest lateral bulge under the posterior border of the postorbital process. Marsh, further, showed this topographical relation in all the other dorsal view figures of braincast in skull: in *Colymbus, Sterna,* and *Ichthyornis* (our figs. 2, 11, and 10).

In the transverse plane of the temporal constriction, in which Marsh's figure ("three-fifth natural size") suggests a maximum cerebral width of 28 mm., the cranium is 30 mm. broad. At the posterior edge of the postorbital process the cranial breadth is 36 mm. Across the tips of the postorbital processes (only the left one seems in place and complete) the breadth is about 43 mm. It follows that maximum cerebral width of *Hesperornis* was at the very least 6 mm. more, and thus more avian in type, than Marsh's reconstruction indicated.

The cranial roof has its highest vault between the postorbital processes. This suggests that here was the highest vault of the cerebrum, avian fashion. However, as the cranium is flattened, this particular roof region may have remained high merely because it is braced by median plus transverse crests. On the ventral side of the specimen, delicate bone has been crushed upward into the brain cavity. Here one can detect a line which possibly was the basis for one line in Marsh's reconstruction of the cerebrum The postero-lateral outline of the hemispheres seems to correspond to the cracks along which the lower wall of the left cerebral chamber broke from the lateral wall, and was pressed up into the cavity. There are somewhat similar cracks on the right side of the specimen. They possibly did have the significance apparently attributed to them by Marsh. The posterior

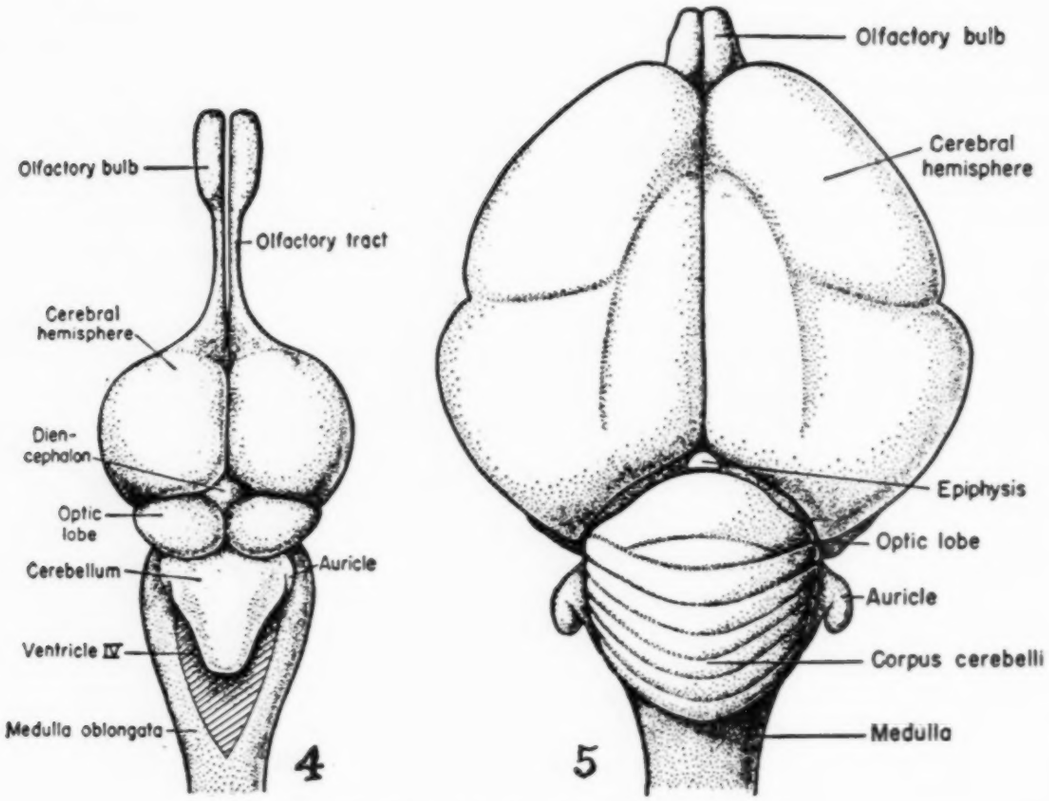


FIG. 4. Dorsal view of brain of alligator. From Romer.
FIG. 5. Dorsal view of brain of goose. From Romer.

margin of the cerebrum may well have lain in the transverse plane next to the posterior end of the temporal fossa. However, even if we agree to fix here the posterior poles of the hemispheres, the holotype would not allow us to measure the length of the post-cerebral brain. In this crushed cranium the occipital plane, which originally faced backward perpendicularly, is so tilted that it continues the dorsal skull surface. Marsh used this deformation in the reconstruction of the *Hesperornis* brain, showing the post-cerebral brain as 23 mm. long. Marsh's reconstruction of the *Hesperornis* skull (pl. XX), however, does not indicate such reptilian proportions since only 16 mm. lie behind the well-marked cerebral capsule.

While in this never-opened cranium it is impossible to detect any endocranial feature except the possible posterior margin of the cerebral capsule, Marsh reported that the cerebral hemispheres "were separated above by an osseous median crest, depending from the roof of the brain case." A median crest, slightly shifted to the right, is indeed partly visible in the ventral aspect of the specimen. It lies, however, between the orbits and was, of course, the upper inter-orbital septum.

The olfactory bulbs of *Hesperornis* lay above the posterior region of the inter-orbital septum and the specimen consequently does not reveal their chambers. When one compares figure 1 with the specimen, one realizes that Marsh saw the septum and used it for reconstructing the bulbi. He concluded that "In *Hesperornis regalis* the olfactory lobes (fig. 1, *ol*) were large and elongate." They appear to have had the amazing length of 16–17 mm., more than double that in the figured endocast of the smaller loon and almost double that in another loon (MCZ no. 772). Even the bulbi of the giant bird, *Aepyornis maximus,* were only 12 mm. long (Edinger, 1942, p. 33). They were

however not as slender and pointed as we believed those of *Hesperornis* to have been. They were blunt cones as in other birds in which the bulbi are particularly well developed, such as the goose (fig. 5). Considering the aquatic habits of *Hesperornis,* one can venture to assume that it did have relatively large bulbi. Küenzi (1918, pp. 50–51) connects the relatively large size of the bulbi in Phoenicopteriformes and Anseriformes with their fishing habits and quotes figures which illustrate the great variations of avian bulbi and cerebra. The weight ratio of bulbi to cerebrum was found to be approximately 1 : 513 in a buzzard, but 1 : 67 in a goose; it would have been even greater in a brain such as figure 1 shows. Küenzi also gives an example of a bird brain with the bulbi exceptionally slender and pointed, *Selenidera* (1918, p. 87, pl. IV). These bulbi compare in length to the cerebrum as 1 : 4.3, and this ratio is 1 : 3.1 in the figured *Colymbus* endocast; but in the *Hesperornis* brain it appears to have been as great as 1 : 1.5.

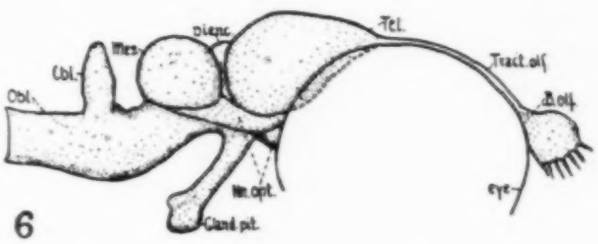
There is no osteological basis for Marsh's giving *Hesperornis* such unavian olfactory bulbs, but there are psychological clues.

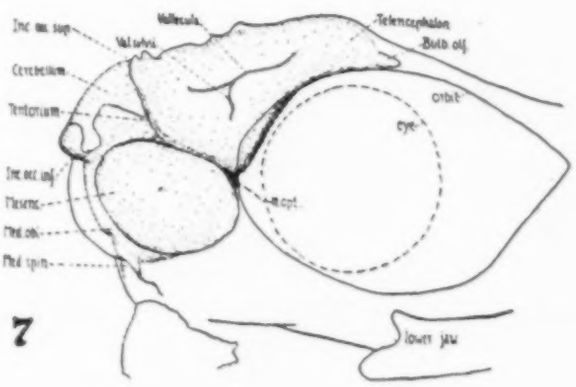
To demonstrate that the *Hesperornis* brain was less avian than reptilian, "The reptilian type is shown on the same page in figure 3, which represents in natural size a cast of the brain-cavity of a young Alligator" (see our fig. 3). In length, at least, the olfactory bulbs of the *Hesperornis* brain reconstruction apparently were meant to correspond to the anterior portion of the alligator cast, labeled "olfactory lobes" (the term until recently often used for the bulbi). This label, however, rests on misinterpretation. The bulbus region of the alligator is not included in that endocast; it lies farther anteriorly (see our fig. 4). The structure which in Marsh's figure of the reptile appears to correspond to the bulbus chamber endocasts of the two birds actually is an endocast of a proximal part of the canal in which the olfactory tracts, coming from the bulbi, approached the cerebrum.

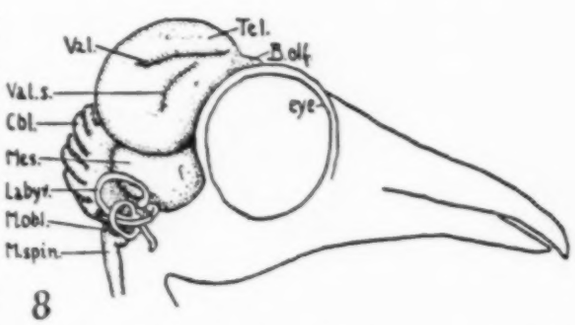
Thus, in drawing the *Hesperornis* bulbi so long, Marsh did not make them "reptilian in type" at all. What he did was to make their length resemble that of the bulbi of an ancient mammal.

It was the brain of *Uintatherium* which had started Marsh's fascination with paleoneurology. As in other early mammals, the cerebrum of the Middle Eocene *Uintatherium* (Marsh 1876) was short, and the olfactory bulbs were relatively enormous. It is amazing to find in Marsh's figures of a *Uintatherium* brain the bulbus to cerebrum length ratio almost the same as in his *Hesperornis* brain, namely, 1 : 1.3. (Likewise, the supposed length proportion of cerebrum to whole brain in *Hesperornis,* 1 : 2.6, is oddly similar to that in Marsh's *Uintatherium,* figure, 1 : 2.4.)

We have at the moment no data relevant to the bulbi of *Hesperornis;* but we can say that it is highly improbable that







FIGS. 6–8. Right side views of brain-eye complex, showing the topographical relations of olfactory bulbs (B. olf.), cerebrum (Tel.), midbrain lobes (Mes.) and cerebellum (Cbl.) in reptilian (6) and avian (7, 8) brain types. From Edinger, 1941. FIG. 6. Primitive extant reptile, *Sphenodon* (× 2). FIG. 7. Flying Jurassic reptile, *Pterodactylus* (× 4). FIG. 8. Extant bird, *Columba* (× ⅝).

bulbi relatively so large as reconstructed by Marsh were present even in a Cretaceous representative of the class in which the sense of smell was reduced.

The plesiotype[4] *and the hindbrain*

The plesiotype occiput alone, of all *Hesperornis* remains, reveals exact information concerning the brain.

This fragment is not what Marsh's legend for its posterior and basal view figures (pl. II, 4 and 5) calls it, viz., "Base of skull," but it contains the posterior end of that. Nor does it, in contrast to plate II, figure 4, have the foramen magnum complete, but Marsh's remark in the legend is true: "Top of cranium broken away." Otherwise this specimen is in excellent condition, being little deformed and cleaned inside, and there are preserved with it three wax- and one plaster-endocast. These casts were taken in 1915. Whether or not Marsh had such an endocast or studied only the interior structure of this fragment, it is obvious that the hindbrain data of the *Hesperornis* figure, allegedly taken from an endocast of the holotype, were derived from the present specimen. In the holotype, the endocranial matrix is *in situ* and thus invisible; but the endocasts of the floccular fossae, conspicuous features of the plesiotype fragment endocasts, are accurately reproduced in Marsh's figure. Further, in the holotype the maximum transverse diameter of the foramen magnum is 9 mm. but in the brain figure it is about 12 mm., as accurately stated of the plesiotype in Marsh's table of measurements (p. 12). As the upper frame of the foramen magnum is flattened down in number 1206 and lost in number 1207, the maximum vertical diameter of the foramen is not known.

The cranial base is preserved forward from the foramen magnum for 19 mm. The lower region of the lateral walls is present to the main trigeminal foramen (fig. 9 V[2,3], broken on the figured right side but a complete foramen on the left side from which we have drawn this region). The basal, paramedian exits of the VIth nerves seem to lie in the splintered transverse break which ends the fragment anteriorly. The specimen thus contains the foramina of all the cranial nerves posterior to V[1]. The upper lateral walls are lacking with the roof. The dorsal gap between the two sides is 7 mm. broad at the foramen magnum, 23 mm. above the floccular fossae, and about 28 mm. at the anterior end of the fragment where the left, slightly distorted wall is preserved higher up than the right one. The endocasts consequently represent a brain surface so oddly limited that to show them in a figure would be puzzling rather than illustrating further the conditions shown in part in figure 9.

It is only a small part of one cranium from which actual data of the *Hesperornis* brain can be gained, but these data are significant with regard to the evolutionary level of the *Hesperornis* brain. A description is given not so much because the

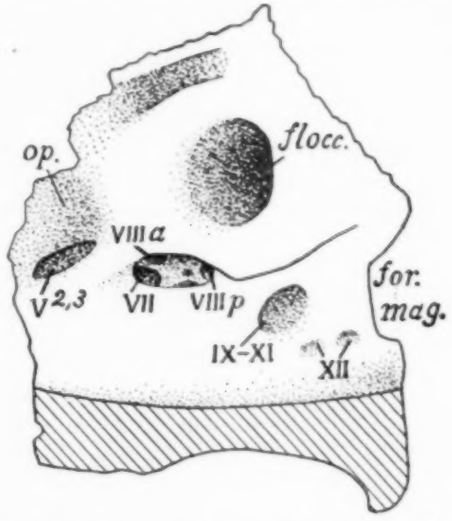


FIG. 9. *Hesperornis regalis*. Right side of cranial fragment YPM 1207, internal aspect (about × 2). Showing: part of the optic lobe pocket; floccular fossa; posterior foramen of trigeminal (V) nerve; internal auditory meatus with foramina for facial (VII) nerve and anterior and posterior rami of acoustic (VIII) nerve; foramen for vagus group (IX–XI) nerves; and the pits around two untraceably small hypoglossal (XII) foramina.

[4] A plesiotype is a specimen figured or described as an example of an already named species.

specimen shows the nerve exits and entrances which were neither mentioned nor figured in the previous description, but because that description is vague and contradicts itself, and the facts support its two minor items but contradict its major statement (which I have italicized): "The cerebellum was quite large, and *reptilian in its general features*. The flocculi were well developed, and lodged in distinct cavities." In contrast to Marsh, I cannot find any reptilian features in this hindbrain of *Hesperornis*.

With regard to the cranial nerve foramina, it is not well possible to distinguish a reptilian type from an avian type of distribution. Naturally, there is no one type in a class as varied as the Reptilia. In *Sphenodon* (Wettstein, 1932, pp. 137–150) there is but one trigeminal foramen, the abducens exit lies far back under the cerebellum, the hypoglossal has three foramina; but in crocodiles (Wettstein, 1937, pp. 312–317) there are a separate V[1] foramen, a more anterior VI foramen, and two hypoglossal foramina as in the birds. Among at least the Recent birds (Kesteven, 1925) the pattern of posterior cranial nerve foramina varies scarcely at all. It is the pattern seen on the endocranial surface of *Hesperornis*. The hypoglossal foramina of birds, in contrast to those of crocodiles, are extremely narrow. In the fossil specimen their position is clearly indicated by pits but I could not find the foramina themselves. Further, Marsh's description of the skull exterior states that "The foramina in the base of the skull have the same general position as in recent Struthious birds" (p. 6).

In their topographical relation to the cerebellum, however, the posterior cranial nerve roots of reptiles are distinctly different from those of birds. The large avian cerebellum overlaps the whole medulla oblongata. In reptiles, not even the helmet-like corpus cerebelli of crocodiles —a vaulted, somewhat lobated sac simulating the avian corpus cerebelli—extends over that part of the oblongata from which emerge nerves IX–XII. Correspondingly (as rightly shown by Marsh in his alligator and loon figures), the posterior oblongata is contained in reptilian endocranial casts as a distinct section, between cerebellum and foramen magnum, but will not show like this in avian endocasts.

The flocculi (auricles), which are connected with the vestibulum of the ear, are in general lacking or minute in the cerebellum of reptiles. Among the reptiles whose actual brains we know, flocculi are distinct lateral lobes only in crocodiles; they do not, however, extend laterad even as far as the lateral circumference of the oblongata, are not lodged in cranial pockets, and hence are not seen in endocranial casts. Among those reptiles whose brains we know only from endocranial casts, flocculi had not been observed in Marsh's times. A beginning of the mammalian flocculus is now known in a mammal-like reptile; I have recently seen in two dinosaur crania shallow concavities which may well be imprints of short flocculi; but floccular structures comparable to those of birds were developed only in pterosaurs. All bird brains have long flocculi, very prominent on the ventro-lateral sides of the corpus cerebelli, usually bent backwards, and extending into special, deep floccular fossae of the cranium.

Both the characters specifically mentioned in Marsh's description of the cerebellum are indicated in the specimen. *Hesperornis* had a large corpus cerebelli and prominent flocculi. This condition is characteristic of birds.

The dorsal outline of the corpus cerebelli (fig. 1) is not actually known. The specimen cannot reveal the anterior relations, length, exact shape, and possible lobulation of the corpus. Maximum breadth was greater than shown in the figure (about 17 mm.), for the much wider cavity above the mouths of the floccular fossae was occupied entirely by the corpus. Another definitely avian feature is made probable by the whole configuration of the endocranial walls and is proven by the position of the floccular

fossae. Their close proximity to the occipital plane shows that the corpus cerebelli of *Hesperornis* had developed well beyond that of any terrestrial reptile, for it extended to the back of the head, avian fashion.

The floccular fossa is as wide and deep as in any Recent bird. Its entrance, 8 mm. anterior to the foramen magnum, is 6 mm. long and 6 mm. high. The fossa extends in a postero-lateral direction over the ear capsule. Its endocast is accurately shown in Marsh's figure. It is 9 mm. long and tapers slightly towards its blunt end. Its large relative size is illustrated by the fact that below the anterior border of the floccular fossae the cast representing the medulla oblongata is 15 mm. broad. The oblongata was, in strong contrast to that of reptiles, narrower than the cerebellum.

At the anterior end of the cranial fragment the lateral walls contain parts of a pair of concavities (fig. 9, *op.*) which extended outward directly above the trigeminal foramen. The break has removed the dorsal and anterior borders of these concavities. It is nevertheless clear that they can only have been the fossae which lodged the optic lobes of *Hesperornis*. The preserved part is on each side in a situation corresponding to the postero-basal region of the optic lobe fossa in the Recent bird skulls I examined, the position shown in Kesteven's figures of the cranial floor and left side wall of *Gallus* (erroneously labeled "fossa lobi olfactorii"; 1925, figs. 1 and 2). We had been misled to believe that in *Hesperornis* "The optic lobes (fig. 1, *op*) were . . . only slightly covered above by the cerebral hemispheres" while there exist no data on their upper borders, and that "Their similarity in size and position to the optic lobes of reptiles is especially noteworthy" (p. 10). The position of the optic lobes is the midbrain roof in reptiles, as in all vertebrates excepting pterosaurs and post-Jurassic birds. In *Archaeopteryx* the avian specialization was apparently not achieved. In the cranial fragment of *Hesperornis*, however, the remains of the optic lobe imprints show that in this Upper Cretaceous bird the lobes were in a lateral or even latero-basal position, in the normal avian correlation with the highly developed cerebellum. At these concavities the preserved portion of the cranial cavity has its greatest width (28 mm.), just as the lower regions of the post-cerebral brain in Recent birds are broadest in the transverse plane of the posterior optic lobe region.

Ichthyornis

The "skulls"

When one has become critical through comparing the concrete data relevant to the *Hesperornis* brain with the status they have been given in the literature, one can only marvel how it was possible that we accepted the "cast of the brain cavity" (p. 121) of *Ichthyornis victor* as a real document of paleoneurology.

A conception of abundant material was created by Marsh's reporting (p. 120) the discovery of "remains representing no less than seventy-seven different individuals of this group of the Odontornithes," that is, of *Ichthyornis* and *Apatornis*. In addition, Marsh's explanation of the figure representing "an outline of the skull of *Ichthyornis victor*, with a cast of the brain cavity in position" (our fig. 10) gave the idea that at least three crania were at hand. Marsh wrote (p. 122) that the cerebral hemispheres "in *Ichthyornis victor* are well shown in figure 29, *c*, which represents a cast taken directly from a cranium with this portion well preserved. . . . The general form and dimensions only of the posterior part of the brain of *Ichthyornis* are shown in figure 29, and hence are indicated by a uniform shading. The outline given was obtained from comparison and measurements of two different specimens."

This "outline" figure is the only dorsal view of an *Ichthyornis* skull. The monograph, so profusely illustrated, contains no ventral view of any skull material. There is only plate XXI, figure 1: "Skull, lateral view, seen from the left, restored

in part." The shaded portions ("the parts preserved") consist of a maxillary fragment and cranium plus orbit roof. The legend to plate XXVI, on which the same skull figure is part of the restoration of the *I. dispar* skeleton, identifies these fragments as the skull remains of the *I. dispar* type (YPM 1450). The only refrence to skull material of *I. victor*, besides that to a cranium in the brain chapter quoted above, and to the quadrate bone in the skull chapter, is not in words but consists of plate XXXIV. This plate shows the skeleton of *I. victor* in left side view. According to the legend, "the shaded portions represent the parts preserved of the type specimen (No. 1452, Yale College Museum), as well as of other individuals."

Am I really the first to see that the main shaded skull portion of Marsh's plate XXXIV is a copy of his plate XXI, figure 1? The figured cranium specimen, allegedly of *I. victor*, has exactly the same extent as that of the *I. dispar* type. From the fragment borders to the smallest details such as the bone sutures, every feature is alike in the *dispar* figure and in the figure presented as that of an *I. victor* cranium. As, apparently, no cranial material of *Ichthyornis* has been discovered since the 1870's, the following specimens are the only ones known to exist.

I. *Ichthyornis dispar*.—(1) YPM 1450. Left side of whole cranium, mostly crushed inward (our fig. 12); now mounted on composite exhibition skeleton. Cracks reveal endocranial matrix *in situ*.—(2) YPM 1459. Small latero-occipital portion with the condyle, and upper rim of right orbit with medially adjacent roof; now mounted with composite *I. victor* skeleton. Neither fragment contains data directly pertinent to brain, but the anterior one indicates avian braincase-orbit complex. "Distance between upper margins of orbits 4.5 mm." (p. 125) in skull reconstructed, on basis of preserved lower jaw, 78 mm. long (pl. XXI, fig. 1; 100 mm. in fig. 29; the skull of the Yale *I. dispar* skeleton reconstruction is 80 mm. long): large eyes have compressed the inter-orbital space.

II. *Ichthyornis victor*.—YPM 1728, now mounted on the exhibition skeleton, is Marsh's "cranium with this [the cerebral] portion well preserved." It is well preserved insofar as it is not crushed. This specimen is, however, not a cranium but is only the lateral wall of much but not all of the right forebrain chamber. The endocast of this fragment, preserved in the Yale collection, is Marsh's "brain-cast." The fragment itself is not figured; it is a thin little shell, whereas Marsh's dorsal view skull reconstruction (our fig. 10) surrounds the *Ichthyornis* cerebrum with thick walls.

The brain

There is no material substantiating Marsh's assertions that the brain of *Ichthyornis* had reptilian characters and that it resembled the *Hesperornis* brain, and no specimen shows the allegedly "most noticeable reptilian features in the two brain-casts . . . the elongated form, and prominent optic lobes" (p. 121). It is not possible to decide whether the brain of *Ichthyornis* was slender as in reptiles or broad as in other birds. We do not know the width of any brain portion because we cannot assume that either of the two preserved brain case fragments of *Icthhyornis* extends to the mid-sagittal plane. The fragments actually existing of the "two brain-casts" cannot demonstrate similarity because they correspond to different regions of the two brains. The *Hesperornis* endocast represents, as we have seen, a hindbrain of definitely avian character. The *Ichthyornis* cast represents a cerebral area too small to warrant interpretation. A brief description of the specimen nevertheless seems in place. Its previous description is in the literature, while actually it cannot reveal whether "The cerebral hemispheres were of moderate size, and proportionably less elongate than in *Hesperornis*" (p. 122).

The endocast of the delicate bone which

laterally enclosed the right cerebral hemisphere of *I. victor* has a smooth, convex surface. Its maximum breadth is 4 mm. As the full breadth of the cerebrum is not known, one is free to speculate that, as figure 10 suggests, 4 mm. was hardly more than half the breadth of the hemisphere. One must then realize that the cast does not comprise that part of the surface which may have contained the characteristic sulcus of bird brains (fig. 8, Vallecula).

The length of this cast is 13 mm. The posterior margin of the hemisphere is not included. The specimen is 8 mm. high posteriorly and tapers anteriorly to 2 mm. height. Apparently the anterior 2 mm. of the cast have a fairly equal height of 2 mm. and a pointed anterior end. This little portion is possibly not part of the cerebral chamber endocast but may represent the lateral surface of the right olfactory bulb. Excepting this region which cannot be interpreted with certainty, the specimen contains no indication of the olfactory bulbs. There does not appear to be any concrete foundation for Marsh's showing the bulbi as well and completely moulded, and 5 mm. long (fig. 10).

The cranial fragment of *Ichthyornis dispar* (fig. 12) is a far better document of paleoneurology than the *I. victor* endocast. Like other small bird skulls (and those of pterodacytyls which in this respect are so characteristically different from other small reptiles in the Solnhofen slates), this *Ichthyornis* cranium was imbedded lying on one side and was flattened laterally during fossilization. This condition lays open the major divisions

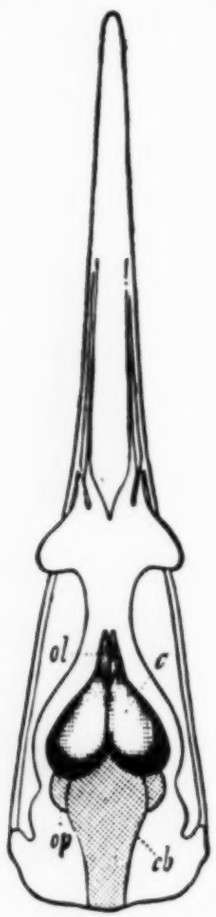


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FIG. 10. "Outline of skull and brain cavity of *Ichthyornis victor* Marsh" (× 1). Fig. 29 of Marsh, 1880.

FIG. 11. Outline of skull and brain cavity of *Sterna* (× 6/5). Fig. 30 of Marsh, 1880.

FIG. 12. *Ichthyornis dispar*, YPM 1450. Posterior parts of skull and lower jaw in reconstruction mount (×2).

and the position in the skull of the braincase which is preserved in its whole antero-posterior extent.

In this specimen indeed "most noticeable . . . are . . . the . . . optic lobes," and it is true that "The optic lobes (fig. 29, *op.*) are very large." They are, however, not "reptilian features;" the midbrain lobes are rather the structure most strikingly avian among the few details recognizable of the *Ichthyornis* brain. They are represented in the specimen by the large oval depression between orbit and occiput. This was the chamber of the left optic lobe. Its lateral bulge is crushed in beyond its frame so we cannot know whether the lobes were "prominent." The latero-basal position contrasts strongly with the dorsal position in standard reptilian brains.

Crushing has set off two other distinct areas of the endocranial cavity. Posterior and dorsal to the optic lobe chamber lies the cerebellar chamber with relatively thick walls. Its shape and position show that a large and vaulted corpus cerebelli occupied and moulded the back end of the braincase. A dent in the dorsal outline of the cranium discloses the fact of cerebro-cerebellar contact and its position above the dorsal tip of the optic lobe. The dent recalls the incisura occipitalis superior of *Pterodactylus* (fig. 7), representative of the only order of Reptilia in which the cerebellum is known to have evolved to such size as to make contact with the cerebrum as in birds. The longest diameter of the *Ichthyornis* cerebellum can be measured approximately as the distance of the dorsal dent from the approximate position of the dorsal rim of the foramen magnum. The length of this oblique axis of the cerebellum, 13–14 mm., is accurately shown in Marsh's figure of this cranium, but in his brain reconstruction (our fig. 10) this length appears as the antero-posterior extent of the post-cerebral brain. The real antero-posterior length of this portion was 6 mm. Its relation to total brain length corresponds to the proportions seen in many Recent birds but not reptiles. The fore-

brain chamber, as far as marked in this *Ichthyornis,* is 12 mm. long.

Anterior and dorsal to the crushed chamber of the optic lobe lies the cerebral chamber. Its contour calls to mind the descriptions of this chamber in birds as "funnel-shaped." Its roof forms the dorsal vault of the skull. The lateral wall is so thin that at first sight I thought I was looking at endocranial cast surface. Nevertheless the posterior region protrudes laterally along the postero-dorsal rim of the orbit. It is less flattened than the other regions of the cranium. This condition indicates the presence, inside the skull, of a broader cavity, braced by more endocranial matrix. In *Ichthyornis,* therefore, the widest part of the brain appears to have been, as in birds, a "temporal lobe." The original width cannot be determined nor, unfortunately, the length of the hemisphere. Cracks above the orbit obscure the region which enclosed the anterior end of the forebrain. The cerebrum is clearly marked for a length of 10 mm. forward from the cerebellum. Continuing this area anteriorly lies a 2 mm.-long, horizontal, tapering cone. I suspect that this represents the left olfactory bulb. Such a bulb would correspond, in relative size and position, to the reduced, supra-orbital bulbus of bird brains. The endocast of *I. victor* suggests a similarly short bulbus. Neither specimen allows one to decide whether this anterior portion of the forebrain chamber did not enclose the anterior pole of the hemisphere rather than the bulbus. In either case it is possible that "The cerebral hemispheres were of moderate size" (p. 122) compared with those of Recent birds. While their length was not, as represented in figure 10, one-third of the brain length, it may still have been only one-half. Measured along its axis, which was steep as in all birds, the total brain of this *Ichthyornis* as far as marked was 20 mm., the cerebrum being 10 (or 12) mm. long.

Possibly because we can "see" this brain only through the sideview of a crushed cranium, the cerebrum appears small, *viz.,* in contrast to the optic lobe. Apparently only half the length of the lobe was overlapped by the cerebrum. In most Recent birds the hemispheres extend farther back, but not in all. I have seen in brains of *Buteo* and *Circus* the same relations as observed in *Ichthyornis,* and some of Küenzi's many lateral views of Recent bird brains also show this condition. The specimen suggests that there was less lateral overlapping of the optic lobe than in those Recent birds with relatively short hemispheres; but post-mortem crushing may be the reason why the lateral view exhibits the whole oval outline of the optic lobe (cfr. fig. 8). Another feature possibly indicating a small degree of cerebral overlapping is the steepness of the optic lobe axis. Küenzi asserts that the position of each portion of the avian brain is dependent on the size of the cerebral hemispheres (1918, p. 72). He found that in Recent birds assigned to a low position in the taxonomic system the cerebrum is small and the axis of the optic lobes steep, and that the "enlarging" cerebrum turns the optic lobe down posteriorly, so that its axis is horizontal in higher-developed bird brains. In extreme cases of this development, the contact between optic lobe and cerebellum is reduced and not visible at all in lateral aspect, whereas that contact is extensive in *Ichthyornis.*

The major portion of the optic nerve tract ends in the surface layer of the highly elaborate avian midbrain lobe, and it is here that in birds the optic nerve makes its main connections. The large size of the optic lobe in *Ichthyornis* can be regarded as indirectly contradicting the previously-held conception that "the olfactory lobes of *Ichthyornis* (fig. 29, *ol*) were large and prominent" (p. 122). When one compares Recent reptilian and bird brains, one feels sure that in avian evolution progressive elaboration of the optic centers must have been coupled with progressive reduction of the olfactory centers. On a small scale such antago-

nistic evolution was observed in the actual phylogeny of two short-lived families of birds; in dinornithids and aepyornithids the olfactory bulbs enlarged while the optic lobes became relatively smaller (Edinger, 1942, p. 43).

The Facts and Their Meaning

The Cretaceous bird brains figured by Marsh as two endocranial casts, which we have seen never existed, have played a large role in discussions of brain evolution because these brains appeared to be unique in their combination of features characterizing today either Reptilia or Aves. Every fact concerning birds of the Cretaceous is important indeed since the fossil record is very poor from this "period of marked evolutionary advance in the class Aves" (Howard, 1950, p. 3).

Altogether four genera of Mesozoic birds are relatively well known, from major remains of the skeleton. They are, first, *Archaeopteryx* and *Archaeornis* which lived about 130 million years ago; second, representatives of a time some 50 million years later, the large diver *Hesperornis* and the small flyer *Ichthyornis*. The two still similar Jurassic forms and the two different Cretaceous forms give us faint glimpses of a long and varied story of which the few details actually told necessarily rank high in evolutionary studies. The general story agrees with theoretical concepts of gradual transformation from reptile to bird. The Archaeopterygiformes had retained many, the Odontognathae only very few of the features whose absence distinguishes Recent birds from Recent reptiles.

In the late Jurassic the plumage appears to have been fully developed, but the wing skeleton was not. Strikingly reptilian are the long tail and the full complement of teeth, the latter, however, being the only feature of the *Archaeornis* skull not occurring in birds of today (Dames, 1884, p. 46). In the *Archaeopteryx* specimen a two-lobed portion of the natural endocranial cast was partially exposed, and its lobes have been interpreted (Edinger, 1926) as a cerebral hemisphere and as an optic lobe which was in a dorsal position. Such a position indicates a condition of the brain far below the evolutionary level of all bird brains now extant. Apparently in *Archaeopteryx* (as in reptiles) the cerebral hemispheres were not developed to such size as to overlap and displace the midbrain (as in birds), nor was the cerebellum. This would agree with the fact that the Archaeopterygiformes were not fully organized as birds. They must have been clumsy flyers, living in trees rather than in the air. It is improbable that they fed in the fashion to which is adapted the brain of Recent birds, which sight from the air and swiftly catch their prey.

The remains of the *Archaeopteryx* endocranial cast and cranium have recently been further prepared and are now being studied by G. R. de Beer. Should the earlier interpretation be found correct, it will show that the brain was one of the several structures slower to change than others during the evolutionary beginnings of the class Aves. The paleoneurology of mammals has shown that brain evolution can lag behind skeleton differentiation in the early history of a group. Mammalia had developed from Reptilia earlier than Aves, yet as late as 55 million years ago, when in the beginning of the Eocene period the different orders were established, at least some Carnivora and Ungulata had similarly short cerebral hemispheres which left the midbrain exposed. The cerebrum, the portion most affected by progressive brain evolution, was slow to assume the morphological and physiological dominance it possesses today in all warm-blooded vertebrates.

We believed that the brains of *Hesperornis* and *Ichthyornis* were further examples of this phenomenon. The present investigation discloses that figures we regarded as showing endocranial cast specimens are almost entirely products of the imagination of Marsh, and upon the basis of his work we have believed that the brains they supposedly represented had

"strongly reptilian" features. Marsh's monograph on Cretaceous birds (1880) is the only extensive treatise on the subject. Short papers by later authors have dealt with some additional discoveries of post-cranial material, with skeleton or skull reconstruction, or with the taxonomic position of the two types. *Hesperornis* and *Ichthyornis* are indeed, as seen by Marsh, so different as to represent two orders, but the osteological and odontological characters in which they are morphologically intermediate between the Jurassic subclass Archaeornithes and modern birds have been recognized as neither so many nor so essential as to warrent their exclusion from the subclass of birds with fully developed wings, united foot bones, etc. Both Cretaceous birds were Neornithes. In *Ichthyornis* but not in *Hesperornis* the presacral vertebrae were still amphicoelous as in Archaeornithes. Both forms had the lower jaws not yet fused and still had teeth in the dentary and maxilla. The premaxilla of *Hesperornis* was already toothless. One finds in the literature the same condition reported of *Ichthyornis,* but actually no premaxillary bone of *Ichthyornis* has been found at all.

The study reported in the present paper was an investigation of the skull remains in search of brain features reflected in the cranium. It has shown that in this respect our information on the structure of the superorder Odontognathae is not adequate; also that complete information is not possible before more material will have been discovered. It is a minor handicap of paleoneurology that frequently one endocranial cast has to be described as "the" brain of a genus, that is, of millions of individuals. Comparative anatomists working with Recent brains also do this, and indeed the main characteristics can be seen in any one specimen. In the case of the Odontognathae, whole brains of which were believed to be known, paleoneurology has had to draw conclusions from two small fragments of endocranial casts and two crushed crania, but not even such poor material is necessarily a major handicap. This study of only parts of brains of two genera has eliminated from the picture we had of Cretaceous birds another supposedly archaic character; their brains were in no way reptilian but were avian in nature.

Only one skull of *Hesperornis* exists in all the world's collections. No endocranial cast has been or can be taken from this specimen. Its cranium indicates that the cerebral cavity was broader by about one-fourth and thus closer to the avian type than shown in Marsh's reconstruction figure. There is no basis for reconstructing the olfactory bulbs as extremely large. An endocranial cast of the only other cranial remains of *Hesperornis* represents most of medulla oblongata and cerebellum, and small parts of the optic lobes. The cerebellum had the extent, the vault and the flocculi characteristic of avian cerebella, and the optic lobes were in the typically avian, lateral position. A similar configuration was developed in only one other group of vertebrates, flyers too, the pterosaurs. *Hesperornis* itself could not fly; the configuration of its hindbrain definitely contradicts Lowe's conclusion from the structure of its skeleton that "there is little reason to think that [*H.*] had volant ancestors" (1935, p. 410).

There is even less skull and endocast material of *Ichthyornis.* It consists of fragments different from the *Hesperornis* remains as to region and preservation. Consequently we have, at present, no material which could show the particular resemblances between the two brains assumed by Marsh. The only *Ichthyornis* endocast is that of a fragment of a forebrain chamber; it represents a lateral portion of a cerebral hemisphere and possibly also of a short olfactory bulb. A second cranial fragment does not reveal data pertinent to the brain, but the third specimen is the left side of a cranium. This is flattened and thus shows the separate chambers which lodged the main portions of the brain but not, of course, their

width. As in *Hesperornis,* every recognizable feature of the brain agrees with the avian type. The cerebellum, regulator of posture and locomotion, was far larger than in reptiles. It overlapped the entire medulla oblongata. It also overlapped baso-lateral optic lobes which were very large, while the olfactory bulbs appear to have been as reduced as in Recent birds. The outline of the forebrain chamber discloses cerebral hemispheres extending back over the midbrain to the cerebellum as in modern birds. The cerebrum, further, was apparently the broadest portion of the brain. The posterior contour of the cerebral chamber indicates however a degree of cerebral overlapping of the midbrain observed in only a few extant birds. The cerebrum bulges farther back in most Recent birds; these, consequently, have reached a higher level of brain evolution than that suggested by the crushed cranium of *Ichthyornis.*

It follows that we have absolutely no data disclosing any reptilian features in Cretaceous bird brains. On the other hand, we know positively that in two birds of 80 million years ago the morphological characteristics of the modern avian brain were achieved in hindbrain and midbrain, and that the forebrain of *Ichthyornis* was distinctly avian in all recognizable features such as the characteristic position in the head and the posterior contact with the cerebellum. There are, further, indications that the olfactory bulbs were reduced. Certainly both the Cretaceous bird brains must have been far more similar to modern bird brains than were the brains of early Tertiary ungulates and carnivores to those of their living descendants. Since we have become acquainted with a transformation of "reptilian" into "avian" brain type, parallel to that in Aves, in both groups of extinct flying Reptilia, it is not surprising to find the avian type fully developed in birds of the Upper Cretaceous, some 50 million years after their ancestors had abandoned terrestrial life. By contrast the early terrestrial mammals, while differently organized than the reptiles they succeeded, took their place also in a geographical sense.

When Marsh described the brain of *Hesperornis,* he stated that there is evidence that in birds "from the Cretaceous to the present time . . . there was a gradual increase in the size of the brain," and he added that "This increase was confined mainly to the cerebral hemispheres, or higher portion of the brain" (pp. 10–11). He thus appeared to have known specimens showing continued progressive brain evolution, of a degree macroscopically observable, throughout the Tertiary epoch. Only a bad picture of only one endocranial cast of a Tertiary bird has ever been published (Gervais, 1859, pl. 49, fig. 2). If Marsh had other material it has never become known. On my recent visit to Paris [5] I have seen Gervais' specimen, an excellent natural endocranial cast from the Gypsum beds of Montmartre (Lab. Pal., Mus. Nat. d'Hist. Nat., AC 7992). It represents a brain of *Numenius* (*Limosa*) *gypsorum* which was formed like the brains of the living representatives of that genus. In a hornbill from the same Upper Eocene stratum, *Cryptornis antiquus* (AC 7991), much of the endocranial matrix is exposed and this, too, is shaped like a fully modern bird brain. Evidently these birds of about 40 million years ago, whose skeletons are quite modern, had also reached the level of brain evolution represented by their living descendants.

Summary

Marsh's figures, allegedly of endocranial cast specimens representing Cretaceous bird brains intermediate between the reptilian and bird types, are reconstructions. Examination of all cranial remains shows that no complete knowledge of the brain forms can be gained from the Cretaceous bird material now at

[5] As a National Fellowship Crusade Fellow of the American Association of University Women.

hand. The cranial and endocast fragments available contain no evidence of the retention of any reptilian brain characters. They show that in *Hesperornis* the hindbrain and midbrain were shaped and arranged as in modern birds, and that in *Ichthyornis* the position of the brain portions relative to each other and to the other head organs was typically avian.

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THE SPONTANEOUS OCCURRENCE OF AMPLIPLOIDY IN SPECIES HYBRIDS OF *GOSSYPIUM* [1]

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INTRODUCTION

The hypothesis of Winge (1917) that constant fertile species might be established by doubling of the chromosome number in interspecific hybrids has been widely confirmed by examples from many genera. Perhaps the earliest case reported is that of *Primula kewensis,* first described by Digby (1912) and later studied extensively by Newton and Pellew (1929). Other genera in which relatively true-breeding, fertile amphiploids have arisen spontaneously from F_1 species hybrids are *Nicotiana* (Clausen and Goodspeed, 1925), *Digitalis* (Buxton and Newton, 1928), *Phleum* (Gregor and Sansome, 1930), *Spartina* (Huskins, 1930), *Brassica* (Frandsen and Winge, 1932), *Triticum* (Berg, 1935), *Rubus* (Yarnell, 1936), *Aegilops* (Kihara, 1937) and *Allium* (Jones and Clarke, 1942). Of intergeneric hybrids, the classic example is *Raphano-Brassica* (Karpechenko, 1927, 1928). Similar doubled generic hybrids were reported in *Aegilops-Triticum* crosses by Tschermak and Bleier (1926) and by Kihara and Katayama (1931).

The existence, in nature and in cultivation, of many species in which the chromosome number is a multiple of the basic chromosome number of the genus has long suggested to observers that some such species may have been formed through a process which occurred spontaneously and which produced amphiploids following hybridization. Among such forms are the 52 chromosome species of *Gossypium,* including *G. hirsutum* L. and *G. barbadense* L., which comprise the American cultivated varieties of cotton. From an extensive study of the chromosome numbers, meiotic pairing and other relationships in the genus *Gossypium,* Skovsted (1934, 1937) postulated that the new world cottons with 52 chromosomes are amphidiploid species, formed by doubling of the chromosome number in hybrids between two 26 chromosome species. Skovsted concluded that the two species involved were representatives of the American wild and Asiatic species of cotton, each of which forms 13 bivalents at meiosis. Studies of meiotic pairing in species hybrids by Webber (1939) and Beasley (1942) confirm Skovsted's observation that the chromosomes of Asiatic and American 26 chromosome species are most nearly homologous with those of the 52 chromosome species. From F_1 hybrids of *G. arboreum* × *G. thurberi,* representatives of the two types of cotton reputed to have given rise to the 52 chromosome species, the production of an allotetraploid has been reported by Beasley (1940c), by Harland (1940) and by Hutchinson, Stephens and Dodds (1945). The interfertility and cytological compatibility of this allotetraploid with *G. hirsutum* and *G. barbadense* (Beasley, 1940c) is additional evidence in favor of Skovsted's hypothesis. Further confirmation of the amphidiploid origin of the 52 chromosome species is found in an accumulation of genetic data by Harland and Atteck (1941) and Harland (1942) involving the identification of duplicate genes in the 52 and in the 26 chromosome species, both American and Asiatic, and the transfer of allelic genes from one species to another. The hypothesis of hybrid origin receives further support from Silow (1946), who describes dupli-

[1] Contribution No. 1367 from the Cotton Improvement Section, Department of Agronomy, Texas Agricultural and Mechanical College System.

cate gene loci in tetraploid species of cotton.

Two amphiploids in *Gossypium* which occurred spontaneously in experimental stocks will be described below. One is especially noteworthy because it possesses two attributes favoring its survival under natural conditions: (1) it is fully self fertile; (2) it has the added advantage of a natural barrier to crossing with species already established.

Origin of Material

The species used in producing the hybrids in which amphiploidy occurred spontaneously are: *G. hirsutum* L., commercial variety Coker 100, with 52 somatic chromosomes; *G. anomalum* Wawra and Peyr., a 26 chromosome species native to Africa; *G. davidsonii*[2] Kellogg and *G. armourianum* Kearney, the latter being two 26 chromosome species native to Baja California (Mexico). The F_1 hybrids, *G. davidsonii* × *G. anomalum*, and *G. hirsutum* × *G. armourianum*, were produced by the late Dr. J. O. Beasley prior to 1942.

In December, 1942, an immature boll was noticed on one of five F_1 hybrids of *G. davidsonii* × *G. anomalum*. At maturity, the boll was intermediate in size, shape and other morphological features between the bolls of the two parent species. The hybrid boll contained five seeds of uniform size. Three seeds planted directly in fine sand failed to germinate, but vigorous plants were obtained from the remaining two, after the seed coats had been removed and the embryos germinated on nutrient agar.

Under similar circumstances, a single boll was harvested in February, 1945, from an otherwise sterile F_1 hybrid of *G. hirsutum* × *G. armourianum*. Of three seeds, a small and a large one with buff colored seed hair contained collapsed

[2] *G. davidsonii* is classified by Hutchinson (Hutchinson, Silow and Stephens, 1947) as a variety of *G. klotzschianum* on the basis of hybridization experiments, which give fully fertile plants in the F_1, F_2 and F_3. For simplicity, the designation *G. davidsonii* will be retained in this article.

Table 1. *Comparison of morphological characteristics of* G. davidsonii, G. anomalum, *F_1 hybrid and the amphidiploid*

	G. davidsonii	*G. anomalum*	F_1 hybrid	Amphidiploid
Leaf shape	entire to three lobed	5 lobed; lobes overlapping	two to five lobed; flat	entire to five lobed; lobes overlapping, less deeply cut than F_1
Leaf color	yellowish green	bluish green	intermediate pale green; thin	pale green; densely covered with stellate hairs; thick
Petal	clear sulfur yellow	cream with lavendar tinge	pale yellow; no lavendar tinge; relatively narrow	intermediate light yellow; broad
Petal spot	brick red	purplish red	intermediate red	intermediate red, very large
Pollen	yellow	cream	rarely shed; light yellow, small, irregular	light yellow, large, uniform
Bracteoles	large, broad, 7 or more teeth	small, linear; 2–3 small teeth	small, narrow, 5–6 teeth	long, relatively narrow, 5 or more teeth
Boll shape, size	as broad as long; 15×15 mm.; 3–5 locules	½ as broad as long; 8×16 mm.; 3 locules	1 boll only produced; like boll on amphidiploid	elongate, pointed, ¾ as broad as long; 14×20 mm.; 4 locules
Boll surface	smooth; glands minute, numerous, inconspicuous	uneven; glands large, conspicuous; 25± per locule		uneven; glands intermediate in number, size and prominence
Seed size and number	broad; 5×7 mm.; 4–5 per locule	pointed; 4×8 mm.; 3–4 per locule		large, broad; 5×10 mm.; 2–3 per locule
Seed coat	dark green seed coat appears naked; seed hairs finely crimped, greenish buff color, 3 mm. long	seed hairs light brown, coarsely crimped, 7 mm. long		light brown or greenish brown seed hairs, crimping intermediate, 9 mm. long

FIG. 1. Flower and leaf of *G. anomalum*, left, and *G. davidsonii*, right.

embryos which did not germinate. One large seed, with a dark green seed coat and greenish seed hairs, contained a large embryo which developed into a strong plant after germination on agar. A year later, a boll containing four large dark green seeds was harvested from a second F_1 of *G. hirsutum* × *G. armourianum*. Plants were grown from two of these seeds and studied cytologically. Two seeds were sacrificed for fiber analysis in another laboratory.

RESULTS

Description of F_1 hybrids and amphidiploids of G. davidsonii × G. anomalum

F_1 hybrids between *G. davidsonii* and *G. anomalum* have been described by Skovsted (1935b) and Amin (1941), who found them to be vigorous, freely flowering but completely sterile, and with most of their morphological characters intermediate between those of the parental species. Following treatment with colchicine, Amin (loc. cit.) obtained fertile F_2 plants which produced a uniform progeny. Hutchison, Stephens and Dodds (1945) mention doubling the chromosome number in a hybrid of the reciprocal cross, *G. anomalum* × *G. davidsonii*.

A comparison of the leaf, flower and fruit characteristics of *G. davidsonii*, *G. anomalum*, the F_1 hybrid and the amphidiploid is given in table 1. Several observations not brought out in the table may be mentioned. The leaves of the original amphidiploid plants and grafts of these upon *G. hirsutum* stock are thick and feltlike to touch, with a coating of stellate hairs so dense along the veins as to make them appear white. Leaves of seedling plants raised from seed of the original amphidiploid are less thick at first, but become thicker as the plants mature. Blossoms of the doubled amphidiploid are larger than those of the F_1, and much larger than those of either pa-

FIG. 2. Flower of F_1 hybrid, left, and of amphidiploid *G. davidsonii* × *G. anomalum* right.

rental species, as may be seen by comparing figures 1 and 2. The style is long, and the stigma extends beyond the staminal column, as in *G. davidsonii*. The original amphidiploids and their progeny exhibit marked periodicity of blooming, especially during the first year of growth, when flowers are produced only during the short winter days. In this respect, the hybrids resemble the *G. davidsonii* parent, since *G. anomalum* blossoms freely at almost any season of

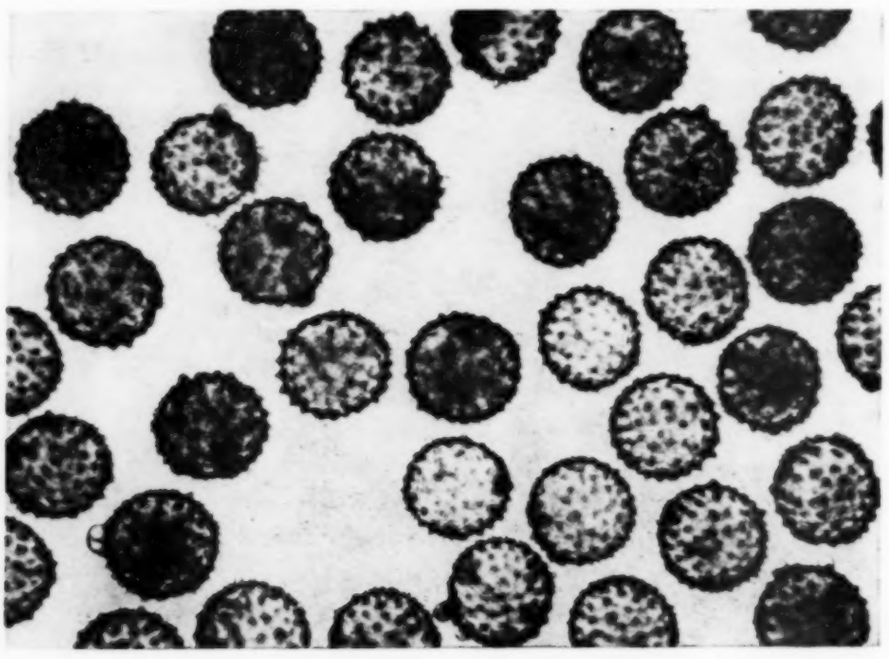

FIG. 3. Pollen of amphidiploid *G. davidsonii* × *G. anomalum*.

the year under local greenhouse conditions. During succeeding seasons of growth the blossoming period of the amphidiploid may be extended into late spring and early summer, later than the flowering period of *G. davidsonii*. F_1 plants which are now more than nine years old may blossom in mid-summer.

In one amphidiploid plant, the period of blossoming was initiated earlier one season by covering the plant with a dark cloth chamber for a period of six weeks in late summer. After treatment, the plant began to blossom in October instead of December as in previous years. Untreated plants blossomed in December.

There is a marked tendency for the F_1 and later generations to shed leaves, buds and flowers when growing conditions, mainly moisture conditions, are not favorable. Such facultative shedding is found in many perennial cotton species, where it serves to restrict fruiting to a more favorable dry period (Harland, 1939; Hutchinson, Silow and Stephens, 1947).

Amin (1941) observed a fertility of 66.3 per cent in colchicine produced amphidiploids of *davidsonii-anomalum*, as measured by a comparison of the number of ovules with number of seeds. In the spontaneous amphidiploid, the number of ovules per locule was 4–5, the number of viable seeds harvested, 2–3 per locule. On this basis the fertility of the amphidiploid is between 50 and 60 per cent on open pollinated bolls in the greenhouse.

Meiosis in F_1 and amphidiploid hybrids of G. davidsonii × G. anomalum

Meiotic pairing of chromosomes in F_1 hybrids of *G. davidsonii* × *G. anomalum* has been studied by Skovsted (1937), Webber (1939), Beasley (1942), and the author, with the results given in table 2. Cytological analysis of the F_1 hybrid on which the fertile boll appeared (Z139–1), noted as "irregular" in an unpublished notation by Beasley, showed a lower degree of metaphase pairing than other F_1 hybrids. Bivalents ranged from 1 to 5 per nucleus, had only one chiasma, and more often appeared as bridges (fig. 4a, b, c). Other F_1 hybrids showed 2 to 12 bivalents, with an average of 4.9. The maximum degree of pairing found by the author in an F_1 hybrid (Z139–4) is shown in figure 4d.

According to Skovsted (1937), chromosomes of *G. anomalum* are larger than those of American wild species, and this observation has been confirmed. Size differences are apparent among the univalents in F_1 *davidsonii-anomalum* hybrids, and some bivalents show asymmetry (fig. 4b, c, d). Univalents are bipartite, but no instances of separating halves of univalents have been observed in these hybrids.

Study of the sporads showed a range of 2 to 10 microspores per sporad in buds of one F_1 hybrid (Z139–1). Only 35 per cent of the mother cells resulted in four microspores, the normal number. Anthers rarely dehisced on F_1 plants of

TABLE 2. *Meiotic pairing in F_1 hybrids of* G. davidsonii × G. anomalum

	Range of II	Total	Average per cell	Chiasma frequency	Range of I	Total	Average per cell	Total PMC
Skovsted, 1937*	0–6	61	3.1	1.08	14–26		19.9	20
Webber, 1939	0–2		0.2		22–26		25.6	40
Beasley, 1942 and unpublished	1–8	100	3.8	**	10–24		18.4	26
MSB Z139–1	1–5	26	2.9	1.00	16–24	182	20.2	9
MSB Z139–4	2–12	109	4.7	1.05	2–22	380	16.5	23
MSB Combined	1–12	135	4.2	1.03	2–24	562	17.6	32

* *G. anomalum* × *G. davidsonii*.

** Unpublished notation: "very rarely bivalents with two chiasmata seen."

FIG. 4a. Metaphase plate of F_1 hybrid of *G. davidsonii* × *G. anomalum* (Z139–1) with 4 attenuated 1-chiasma bivalents and 18 univalents.

FIG. 4b. Metaphase plate of F_1 hybrid of *G. davidsonii* × *G. anomalum* (Z139–1) with asymmetrical bivalent and 24 univalents.

FIG. 4c. Metaphase plate of F_1 hybrid of *G. davidsonii* × *G. anomalum* (Z139–1) with 3 1-chiasma bivalents and 20 univalents.

FIG. 4d. Metaphase plate of F_1 hybrid of *G. davidsonii* × *G. anomalum* (Z139–4) with 12 bivalents and 2 unequal univalents. One bivalent has two chiasmata.

davidsonii-anomalum, but shedding anthers were found on one or more flowers on four F_1 plants. Examination of pollen shed by flowers of two hybrids showed from 70 to 90 per cent of small or misshapen grains. Several sizes of large grains, equal in size to those of normal tetraploid cotton, or larger, formed the remaining 10 to 30 per cent.

Meiotic pairing proved to be similar in the two plants grown from seeds produced on the F_1 hybrid, and the data are combined in table 3. Nine of 23 nuclei had 26 bivalents (fig. 5a), proving the plants to be amphidiploid. Several nuclei had 2 to 4 univalents (fig. 5b), and in others a trivalent or quadrivalent (fig. 5c) was present. Most bivalents appeared nor-

TABLE 3. *Meiotic pairing in the amphidiploid* G. davidsonii × G. anomalum

Configurations	Number of PMC
26 II	9
25 II 2 I	6
24 II 1 IV	2
24 II 1 III 1 I	2
24 II 4 I	3
23 II 1 IV 2 I	1
Total	23

mal, with two chiasmata (fig. 5a, b, c). The number of bivalents averaged 25.0 with 1.94 chiasmata per bivalent. The formation of quadrivalents and the departures from regular bivalent pairing in the amphidiploid can be attributed to the partial homology existing between chromosomes of *G. davidsonii* and *G. anomalum*, as evidenced by the pairing found in the F_1 hybrid.

In the amphidiploids 90 to 98 per cent of the sporads appeared normal, with 4 uniform microspores. The remainder had 6 to 8 microspores, with one bud having a range of 2 to 12. Mature pollen, which was shed abundantly, was uniform in size and shape (fig. 3). The diameter was about 124 microns, which is within the normal range of the pollen of the natural amphidiploid, *G. hirsutum*.

Seeds from the original *davidsonii-anomalum* amphidiploid have germinated under natural conditions in the soil. Plants of the succeeding generations show no segregation and have a fertility equal to that of the original amphidiploids. Meiotic metaphase nuclei have 22 to 26 bivalents, usually 24 to 25, sometimes with a quadrivalent or two univalents, as in the original amphidiploids. At anaphase of the first division, one case of 27–25 separation was observed.

Fertility tests of F_1 G. davidsonii × G. anomalum *and other* F_1 *hybrids*

As a test to determine whether unreduced restitution nuclei are formed with any considerable frequency during macro- and microsporogenesis in *Gossypium*, several types of crosses were attempted. Pollen of F_1 *davidsonii-anomalum* flowers with dehiscent anthers was applied to stigmas of emasculated flowers of the amphidiploid. No bolls developed. As noted above, only 10 to 30 per cent of

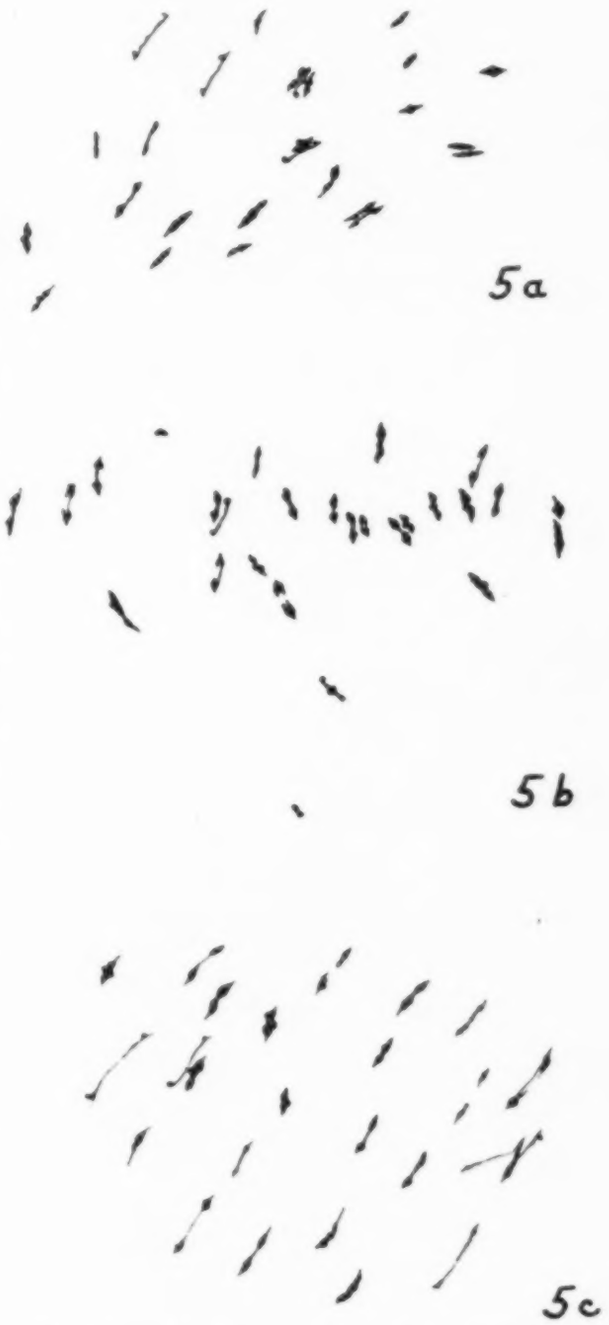

FIG. 5a. Metaphase plate of amphidiploid *G. davidsonii* × *G. anomalum* with 26 bivalents.

FIG. 5b. Metaphase plate of amphidiploid *G. davidsonii* × *G. anomalum* with 25 bivalents and 2 univalents.

FIG. 5c. Metaphase plate of amphidiploid *G. davidsonii* × *G. anomalum* with 24 bivalents and 1 quadrivalent.

the pollen of these flowers appeared normal. The reciprocal test was made using the F_1 hybrid as ovule parent. Thirty-eight pollinations were made using pollen of the amphidiploid *davidsonii-anomalum;* seventeen, with pollen from *G. davidsonii,* and nine each with pollen from *G. anomalum, G. klotzschianum* and miscellaneous 4x species and hybrids. Most bolls were shed in 3–5 days, and none matured.

In a further attempt to recover possible restitution nuclei formed during macrosporogenesis, 176 flowers of the following F_1 hybrids were pollinated with *G. hirsutum* pollen: *G. hirsutum* × *G. thurberi,* 38; *G. hirsutum* × *G. armourianum,* 96; *G. hirsutum* × *G. anomalum,* 12; *G. hirsutum* × *G. arboreum,* 21; *G. hirsutum* × *G. sturtii,* 7; *G. anomalum* × *G. thurberi,* 2. No mature bolls were harvested on any of these hybrids.

Incompatibility of G. davidsonii × G. anomalum *hybrid*

All attempts to cross *G. davidsonii* with *G. hirsutum* failed, as has been the experience of other investigators (see below). The cross *G. hirsutum* × *G. davidsonii* produced bolls which were shed prematurely or which contained many empty seeds. Of 49 seeds containing small embryos, 17 germinated on nutrient agar. Four of these grew enough to be transplanted to soil, and these died in the cotyledon stage. When mixed pollinations (Beasley, 1940b) were made, using pollen of a strain of *G. hirsutum* carrying a dominant gene for red plant color, only non-hybrid seedlings survived.

G. anomalum, on the other hand, has been widely crossed with both diploid and natural amphidiploid species. On the chance that the incompatibility of the *G. davidsonii* genome might be counteracted by the *G. anomalum* genome, the cross compatibility of the amphidiploid *davidsonii-anomalum* was tested in several types of crosses. Reciprocal pollinations with *G. hirsutum* were made. When the amphidiploid *davidsonii-anomalum* was used as female, all bolls were shed unless pollen of the hybrid also was applied. All bolls so produced contained large and small seeds. The large seeds in all cases were selfs; the small seeds contained small embryos which failed to germinate when excised and planted on agar.

The cross *G. hirsutum* female × *davidsonii-anomalum* amphidiploid male produced bolls which generally were shed after 8 to 10 days. Fifteen bolls which matured contained empty seeds. Of six plants grown from as many seeds in three bolls, five proved to be normal *G. hirsutum.* One seed, from a boll containing this seed only, produced a slow growing plant which proved to be approximately 2N + 15, or hyperploid *G. hirsutum,* with many trivalents and univalents. The possibility that this plant, like similar plants in the progenies of intergeneric or incompatible crosses, is the result of apomictic development, is discussed elsewhere (Brown, in press).

By crossing synthesized amphidiploids, it has in some instances been possible to combine two diploid species which have not been crossed directly (Brown, 1949). Attempts were made to cross the amphidiploid *davidsonii-anomalum* with other amphidiploids and trispecies combinations which have been synthesized from species hybrids. These included the following: *arboreum-thurberi, arboreum-anomalum, arboreum-stocksii, arboreum-thurberi-hirsutum, arboreum-thurberi-barbadense,* and *arboreum-stocksii* × *arboreum-anomalum.* Many pollinated flowers and immature bolls fell. Bolls which matured contained mostly empty seeds, but a few seeds contained embryos. Of 122 excised seeds, 37 produced seedlings which died in the cotyledon stage. Ten seedlings resulting from crosses using self and outcross pollen proved to be selfs. Two plants, from *arboreum-thurberi-barbadense* × *davidsonii-anomalum,* developed true leaves before dying. With this exception, the amphidiploid *davidsonii-anomalum,* like the species *G. davidsonii,* has failed to produce plants which survive beyond the

cotyledon stage when crossed with other species or hybrids. The incompatibility of this amphidiploid with other hybrids is undoubtedly due to the presence of the *G. davidsonii* genome. Despite this incompatibility, the amphidiploid has been successfully grafted onto *G. hirsutum*.

A few attempts were made to backcross the amphidiploid with its diploid parental species, *G. davidsonii* and *G. anomalum*. All such flowers fell shortly after pollination.

Description of F_1 and amphiploids of G. hirsutum × G. armourianum *and cytology of the amphiploids*

F_1 hybrids of *G. hirsutum* × *G. armourianum* have a growth habit suggestive of the wild parent, with many branches which tend to grow downward. The leaves are glabrous and aromatic. They are entire to three lobed in shape, and are intermediate in size between those of the two parental species. Flowers have light yellow petals with deep red petal spots, red filaments and anther sacs, and yellow pollen.

At first slow growing, the seedlings obtained from the open pollinated bolls on the untreated F_1 hybrids developed into strong plants. At maturity they were indistinguishable from 4 plants obtained from bolls produced on colchicine treated grafts of similar hybrids. The leaves were glabrous like those of *G. armourianum* and approached those of *G. hirsutum* in size, but had fewer lobes and were less deeply cleft. Flowers were larger than on the F_1 and shed pollen more freely.

F_1 hybrids of *G. hirsutum* × *G. armourianum* usually form 13 bivalents and 13 univalents at metaphase I, although Webber (1935) occasionally found quadrivalents, and Skovsted (1937) found trivalents.

Upon cytological analysis, two plants which were grown from seeds from untreated F_1 hybrids proved to be 6x, having 78 chromosomes. Combined data from both plants are given in table 4.

TABLE 4. *Meiotic pairing in spontaneous hexaploids, from untreated F_1 hybrids of* G. hirsutum × G. armourianum

	II	III	IV	I	No. PMC
	15		12		2
	19		10		3
	20	3	7	1	1
	20		9		1
	22		8	2	1
	22	2	6	2	1
	23		8		2
	24	1	6	3	1
	25	2	5	2	1
	25		7		1
	25	1	6	1	1
	26		6		1
	26	2	5		2
	27		6		3
	29		5		2
	29	2	3		1
	29	1	3	5	1
	30		4	2	1
	30	1	3	3	1
	30		4		1
	31	1	3	1	2
	33		3		1
	35		2		2
	35		1	2	1
	35		1	4	1
	35	2		1	1
	36		1		1
	36	2		1	1
	37	1		1	2
	38			1	1
Total	1135	25	201	34	41
Average	27.68	0.61	4.90	0.83	

Calculations based on 41 plates gave averages of 27.68 bivalents, 4.90 quadrivalents, 0.61 trivalents, and 0.83 univalents. Comparable averages calculated from 39 plates of four seedling hexaploids from colchicine treated F_1 hybrids were as follows: 26.68 bivalents, 4.43 quadrivalents, 1.66 trivalents and 1.77 univalents. The range of bivalents was 18 to 35; of quadrivalents, 0 to 9. The slightly higher frequency of trivalents and univalents in the spontaneous hexaploids is not deemed significant considering the spread in the number and type of configurations found in the number of plates analyzed.

In all hexaploids the number of trivalents was less than the number of quad-

rivalents, thus keeping the number of univalents low. The calculations include a number of plates in which one or two chromosomes were unaccounted for. No configurations higher than quadrivalents were found in any plant. Several aberrant plates, not included in table 4, were seen in the spontaneous hexaploids. Seven plates contained less than 78 chromosomes; one had 52, six had 69–74 chromosomes. Two plates had more than the hexaploid number, there being 81 and 82–83 chromosomes, respectively.

Iyengar (1944), in a colchicine produced hexaploid of *G. barbadense* × *G. armourianum*, found an average of 32.75 bivalents, 0.86 trivalents, 1.75 quadrivalents, 0.02 pentavalents, 0.04 hexavalents and 2.32 univalents in 28 plates.

Metaphase plates of *hirsutum-armourianum* hexaploids, like those of any hexaploid involving the D genomes,[3] have many small configurations which are subject to two interpretations, either as quadrivalents formed by two bivalents joined by a single terminal chiasma, or as two pairs of bivalents showing close secondary association. The configurations in question are invariably small, involving chromosomes of the D genomes only. In a preliminary study of one hexaploid there were frequently three or four such ambiguous configurations in one nucleus, and in one plate, as many as seven. A maximum of three unequivocal quadrivalents was found in these plates. When doubtful configurations were interpreted as quadrivalents, the maximum rose to eight; the number of bivalents was reduced correspondingly. Such differences in interpretation, as well as chance variation in the material at the time of collection, may contribute to differences in pairing data from similar hybrids by different investigators. Since in the triploid hybrid the maximum of 13 bivalent associations is usually realized, a maximum of 13 quadrivalents in the hexaploid is theoretically possible. This maximum has never been reported, which indicates that differential affinity as well as competition may play a role. However, the maximum association theoretically possible in autopolyploids is likewise seldom, if ever, realized. Whether interpreted as secondary association or true quadrivalents, the four chromosome associations found in the *hirsutum-armourianum* hexaploid are similar to many similar configurations commonly found in autopolyploids. They thus serve to supplement the evidence derived from the study of F_1 hybrids that the chromosomes of *G. armourianum* are closely related to the D genome of the *hirsutum* complex.

Pollen shedding was irregular on spontaneous and induced hexaploids, and varied from flower to flower. Pollen grains were of three sizes: large grains, 136–149 microns in diameter, a size characteristic of *Gossypium* polyploids higher than tetraploids; medium grains, 112–124 microns, the size usually found in natural tetraploid cotton; and small or misshapen grains, 100 microns or less. Small or abnormal pollen grains constituted more than 75 per cent of the pollen grains examined. None of the plants have produced selfed progeny but pentaploid progeny have been obtained from back-crosses to *G. hirsutum*. Also, double pentaploid plants, containing genomes of two diploid species, have been obtained when the *hirsutum-armourianum* hexaploids were crossed with hexaploids involving other diploid species. These include crosses of the *hirsutum-armourianum* hexaploid with *hirsutum-herbaceum*, *hirsutum-arboreum*, *hirsutum-sturtii* and *hirsutum-stocksii hexaploid* male; and reciprocally, *hirsutum-armourianum* hexaploid male with *hirsutum-herbaceum*, *hirsutum-anomalum* and *hirsutum-stocksii* hexaploid female.

[3] The genome symbols used in this paper are those devised by Beasley (1940a). The letters A, B, C, D and E designate the genome groups in *Gossypium* which are well differentiated cytologically as well as genetically. $(AD)_1$ and $(AD)_2$ represent the genomes of the natural amphidiploids *G. hirsutum* and *G. harbadense*, respectively.

Discussion

Origin of the amphiploids

The initiation of fertile amphiploid forms following doubling of the chromosome number in all or part of the somatic tissues in species hybrids has been described in *Nicotiana* (Clausen and Goodspeed, 1925), *Fragaria* (Ichijima, 1926), *Primula* (Newton and Pellew, 1929), *Brassica* (Frandsen and Winge, 1932), *Aquilegia* (Skalinska, 1935) and possibly *Rubus* (Yarnell, 1936). In other forms, such as *Digitalis* (Buxton and Newton, 1928), *Phleum* (Gregor and Sansome, 1930), *Triticum* (Berg, 1935) and *Raphano-Brassica* (Karpechenko, 1927), there is evidence that restitution nuclei are formed during gametogenesis.

Evidence that restitution nuclei are formed in any significant frequency in sterile F_1 species hybrids of *Gossypium* is lacking. Data from many different F_1 species hybrids are negative, pollination of such hybrids in an attempt to recover possible restitution nuclei in ovules having proved fruitless. Pollination of a limited number of flowers of the *davidsonii-anomalum* amphidiploid with pollen from like F_1 hybrids, to recover restitution nuclei formed during microsporogenesis, has likewise proved unsuccessful.

Under local conditions *hirsutum-armourianum* F_1 hybrids have been completely sterile when backcrossed to *G. hirsutum* or left to open pollination. However, Skovsted (1935b) described the F_1 of *G. barbadense* × *G. armourianum* as partly fertile in backcrosses to *G. barbadense*. Webber (1935) described hybrids of *G. hirsutum* × *G. armourianum* as forming seedless capsules, but later Webber (1939) grew seven plants from selfed and open pollinated seeds of similar hybrids. One plant resembled the intermediate F_1 and six resembled *G. hirsutum*. Fertility ranged from 0 to 85 per cent in these plants. The chromosome number was not reported, but there was no indication in either instance that restitution nuclei were a factor in the infrequent cases of partial fertility of the F_1.

It is evident from the cytological analyses and the observation of phenotypic characters of the two spontaneous amphiploids, *davidsonii-anomalum* and *hirsutum-armourianum*, that the initial fertile ovules in each hybrid must have been fertilized with self pollen. In the case of *davidsonii-anomalum*, with a manifest incompatibility with other hybrids and species, no other compatible pollen was available. The formation of bolls containing four or five seeds must have required the formation of numerous gametes, both male and female, each containing the unreduced hybrid complement. In the absence of a known agent which might affect the maturation process, the probability of the simultaneous formation of multiple restitution nuclei during both macro- and microsporogenesis is so improbable as to rule out this phenomenon as an explanation. The simplest explanation for the formation of the fertile bolls would therefore be pre-meiotic doubling of somatic tissue, possibly in the bud primordium, followed by normal reduction during meiosis. The number of seeds per boll on both F_1 hybrids, and the similarity in meiotic behavior in the two original amphidiploids of *davidsonii-anomalum*, support this view.

The incompatibility of the davidsonii *genome*

Although hundreds of attempts have been made, the species *G. davidsonii* has been hybridized with few other species in the genus. The species other than *G. anomalum* with which *G. davidsonii* has been successfully crossed include *G. sturtii* (Skovsted 1935a) and *G. klotzschianum* (Webber 1939, and others), the latter closely related to *G. davidsonii*. Silow (1941) obtained sterile combinations between *G. davidsonii* and backcross derivatives from *G. anomalum* × *G. arboreum* or *G. herbaceum*. Webber (1939) indicated that *davidsonii* may be combined

with *G. armourianum* or *G. harknessii* in triple hybrids involving *G. thurberi.*

Among the species with which *G. davidsonii* fails to cross are *G. herbaceum, G. arboreum* (diploid and tetraploid), *G. thurberi, G. armourianum, G. harknessii, G. aridum, G. raimondii, G. stocksii, G. hirsutum,* and *G. barbadense.* One or more of these species has been tested by many investigators, including Harland (1928), Harland and Atteck (1931), Skovsted (1935b), Webber (1939), Stephens (1942, 1945) and the author. When crossed bolls involving the above species are not shed before maturity, either the seeds are empty, or the hybrids die in the cotyledon stage.

Following a study of certain F_1 hybrids, which failed to explain the incompatibility of *G. davidsonii* with other American species on a cytological basis, Skovsted (1937) ascribed the incompatibility to complementary factors. Silow (1941) suggested that the ability to hybridize may be influenced by general genotypic balance, rather than a simple gene mechanism such as is concerned in the complementary lethal system. Stephens (1942) discussed cross compatibility in the genus *Gossypium* from the standpoint of endosperm/zygote ratios, but found that *G. davidsonii* failed to conform to the general scheme and must involve an additional genetic or physiological factor. Stephens (1945) attributed the failure of *G. davidsonii* to hybridize with other species to a gradual differentiation of parental types, resulting possibly in a fundamental disharmony between hybrid zygote and surrounding tissues.

The incompatibility of the *davidsonii-anomalum* amphidiploid with *G. hirsutum* and with other amphidiploids can be attributed to the presence of the *davidsonii* genome. The survival of combinations of this amphidiploid with other hybrids to the cotyledon stage indicates that the incompatibility lies, not in a failure of fertilization, nor in an unbalance between zygote and maternal tissue, but in a post fertilization disharmony, or general zygotic unbalance.

Dilution of the *davidsonii* genome to one-fourth of the zygotic complement fails to overcome this incompatibility. Even where the possibility of segregation exists, as in trispecies hybrids, namely *arboreum-thurberi* × *hirsutum* or *barbadense,* and *arboreum-stocksii* × *arboreum-anomalum,* no compatible combinations have been obtained. Were a limited number of complementary genes concerned, gametic types compatible with *G. davidsonii* might be realized through segregation.

The significance of spontaneous amphiploidy in Gossypium

Although doubling the F_1 hybrids to produce amphiploids is not a new phenomenon, its spontaneous occurrence in the genus *Gossypium* is of added interest because it is a recurrence of what must have occurred earlier to produce the cultivated American species. The actual time and locale of the initial doubling, and whether it occurred once or often to produce the diversified and often intergrading forms at present classified as *G. hirsutum* and *G. barbadense,* and the isolated *G. tomentosum,* are still in doubt. But the simplicity with which spontaneous doubling occurred in the present hybrids adds weight to the hypothesis of the origin of the natural amphidiploids.

The new *davidsonii-anomalum* amphidiploid is ideally equipped to establish itself as a new species in a suitable environment. It is highly self fertile, and produces a vigorous perennial plant. As an amphidiploid, it is isolated from its parental species and other diploids by a difference in chromosome number. Furthermore, it is isolated from any competing amphidiploid species by a genetic barrier, the incompatibility of the *davidsonii* genome.

The species *G. davidsonii* now occupies a restricted range on the shores of the Gulf of California and adjacent islands. Its close relative *G. klotzschianum* is limited to the Galapagos Islands. *G. ano-*

malum, however, is the most widespread of the wild diploids, and has a long blooming period uncomplicated by day length requirements. The amphidiploid of *davidsonii* and *anomalum* should therefore have a greater range of adaptability than that of *G. davidsonii*, and perhaps *G. anomalum* also. The amphidiploid should be a blend of the physiological characters no less than of the purely morphological characters of the two parental species. Although amphidiploids tend to intermediate development of species characters, exceptions can be found. The seed of the *davidsonii-anomalum* amphidiploid is larger, and the seed hairs are longer, than the corresponding characters in either parent species. What significance this may have for the development of lint in the cultivated amphidiploid species is problematical.

The ability of allopolyploids to spread beyond and outlast their parental species has been pointed out by Huskins (1930) and stressed particularly by Stebbins (1947). The phenomenon is in fact well illustrated in the genus *Gossypium* by the natural amphidiploid *G. hirsutum*. The species has spread far beyond the present range of not only the American wild species but of the cultivated Asiatic species as well. Under cultivation, *G. hirsutum* is not only competing with, but replacing, the cultivated Asiatic species to a large extent in India, China and Africa. According to Hutchinson and Ghose (1937) and Hutchinson, Silow and Stephens (1947), upland cottons have persisted as admixtures in unselected crops of *G. arboreum* in central India for a century. In the New World, strains of *G. hirsutum*, relics of earlier cultivation now abandoned, have become established as "wild" cotton in the natural vegetation. *G. hirsutum* var. *marie-galante* is still found in the West Indies, and *G. hirsutum* var. *punctatum* on the coast of the Gulf of Mexico. These instances indicate that cultivation is not absolutely necessary for the survival of strains of *G. hirsutum* which have not been selected too rigidly for annual habit and early maturity.

The amphidiploid *davidsonii-anomalum*, like *G. hirsutum*, is a combination of Old World and New World species. The ranges of these species involve a maximum of geographical isolation; phylogenetically, the species therefore represent very early lines of divergence from a common ancestor. In their present state they represent extremes of genetic and cytological differentiation. The combination of two such species should therefore be a most promising one for the production of a successful polyploid.

It is highly probable that pairing is rarely perfect in the original amphidiploid produced by doubling of the chromosome number in a species hybrid. Howard (1938) and Sears (1939) have described how bivalent formation between partially homologous chromosomes in an F_1 hybrid may result in structural changes which lead to imperfection in the subsequent amphidiploid condition, as revealed by univalent or polyvalent formation. Where doubling occurs in premeiotic stages, such non-homology is not expected, and any irregularity found in amphidiploids resulting from somatic doubling can usually be explained by partial homology between chromosomes of the parental species.

Although pairing was appreciably reduced in the particular F_1 plant of *davidsonii-anomalum* on which the fertile boll was produced (table 2), pairing in sibling hybrids indicates that partial homology exists between many chromosomes of the two parent species. The irregularities in meiosis found in the amphidiploid can be attributed to such interspecific homology. The maximum deviation from 26 bivalents found in the amphidiploid is one quadrivalent and two univalents. Granting that differential affinity may play a role here, it is nevertheless demonstrated that the interspecific homology is sufficient to furnish competition between two or three pairs of chromosomes only. When partially homologous chromosomes from different species form bivalents in

the amphidiploid, their actual homologues may be left unpaired. The difference in size of the univalents sometimes found in the amphidiploid (fig. 4d) shows that a limited amount of such interspecific pairing does occur. However, the uniformity of the F_2 from selfed seed of the amphidiploid indicates that interspecific pairing is not frequent enough to lead to segregation in the F_2 as in certain other forms, e.g. *Crepis* (Poole, 1931) and *Aquilegia* (Skalinska, 1935). Such segregation, as has been pointed out by Darlington (1937), occurs more often in amphidiploids obtained from F_1 hybrids which are at least partially fertile.

A further explanation for the uniformity of the F_2 is that segregates which might involve duplication or loss of all or part of a chromosome from either parent species might be eliminated, if not in the gametophyte, in the early zygote stage. Pollen of the amphidiploid is apparently all morphologically good. If the ovules are likewise all viable, the difference between number of ovules and number of seeds harvested may mean zygotic elimination. Although the absolute number of offspring may be reduced by such zygotic selection, the decrease is compensated for by the better genetic balance which is thereby assured in the survivors; the incipient species is not handicapped by a multitude of unbalanced segregates of questionable value for the perpetuation of the strain.

As noted above, there are residual homologies between the B and D genomes, leading to interspecific pairing in the F_1 and the amphidiploid. Likewise, there is pairing between the A and D genomes, which like B and D have evolved independently of each other. However, the (AD) complex of the natural amphidiploids is now functionally diploid, with less pairing between A and D in haploids of *G. hirsutum* or *G. barbadense* (Beasley, 1942, and others) than between A and D in the F_1 hybrids of *arboreum-thurberi* (Skovsted, 1937; Beasley, 1942). Differentiation must have occurred to decrease whatever initial homology may have existed between A and D at the time of the origin of the original F_1 and of its doubling to change the allotetraploid 2(AD) into a functional diploid. In the same way, other amphidiploids which originally have some competitive interspecific pairing may become functional diploids. The few chromosomes which are involved in multivalent formation in the *davidsonii-anomalum* amphidiploid might be expected to undergo eventual structural differentiation. By selection analogous to that having occurred in (AD), a fully fertile, cytologically regular amphidiploid of *davidsonii-anomalum* could evolve.

It is improbable that evolution proceeding independently in the A and D genomes has increased the homology between them, leading to pairing in the F_1. It is more probable that the homologies common to A and D have decreased as the species became differentiated, and that the homologies still present have persisted since the separation of the two genomes.

The species *G. hirsutum* cannot be exactly duplicated by crossing two present day A and D species. The precise diploid species which produced the original amphidiploid (or amphidiploids) which evolved into *G. hirsutum*, *G. barbadense* and *G. tomentosum* may no longer exist. Present diploids, especially in the New World, occupy isolated habitats of limited extent. If the ranges were once contiguous, intergrading forms may have existed in the regions now devoid of cotton species. On the other hand, it must be borne in mind that unless the origin of the natural amphidiploids is very recent, not only the original amphidiploid, but the parental diploids as well, have had time to evolve. There was no selection pressure to differentiate between the A and D genomes as long as they were separated by an ocean; whatever cytological differences became established were due to non-selective accumulation. In the amphidiploid there was selection pressure for differentiation between A and D. This means that the A and D genomes

have undergone differentiation independently in the initial species; in the amphidiploid, they were subject to a selection which tended to eliminate any residual homology between them. In other words, differentiation between A and D was subject to different pressures within the amphidiploid and in geographically isolated diploids. The initial genomes found in polyploids may thus be subject to evolution partially independent of species evolution.

Unlike the *davidsonii-anomalum* hybrid, the *hirsutum-armourianum* amphidiploid is unlikely to become a true-breeding species without extensive differentiation and selection. It was derived, not from two diploids, but from two species one of which was already amphidiploid. *G. hirsutum,* although functionally a diploid so far as its own gametes are concerned, is phylogenetically an allotetraploid, with one genome similar to the *armourianum* genome. The hybrid combination therefore involves two genomes which pair regularly in the F_1, with the consequence that pairing in the new amphiploid is complicated by quadrivalent formation. It is not surprising, therefore, that the hexaploid is of low fertility. Theoretically, by differentiation of the two D genomes a true-breeding hexaploid could evolve. This process would require a long period of random mutation and selection, and in the meantime natural selection would be acting in other directions.

The *hirsutum-armourianum* hexaploid, again unlike the *davidsonii-anomalum* amphidiploid, is not isolated from *G. hirsutum.* It is therefore subject to backcrossing as well as outcrossing. Although some D pentaploids (e.g. *raimondii* and *thurberi*) are partially fertile either as male or female, the *armourianum* pentaploids are fertile only as male. Whereas the progeny of backcrosses from pentaploid females range from tetraploids to pentaploids, the backcross progeny from pentaploid males is limited to tetraploids and hypertetraploids with one to three extra chromosomes (Beasley and Brown, unpublished). By selfing, it is possible to recover strains with 27 pairs of chromosomes from trisomics (Beasley and Brown, 1943; Brown, 1949), but these are not completely stable and some are of reduced fertility.

From backcrosses of hexaploids to *G. hirsutum,* characters of the diploid involved in the hexaploid have been retained, not only in trisomics and tetrasomics, but in completely tetraploid lines.[4]

The rapid return of a hexaploid line to the tetraploid condition following backcrossing is accompanied by restoration of high fertility. The amount of germplasm from a diploid which can be incorporated into tetraploid strains from backcrosses of a hexaploid will depend upon several factors: namely, the amount of interspecific pairing, the randomness of segregation of the chromosomes in quadrivalents, the amount of crossing over, and the degree to which whole chromosomes and chromosome segments can be substituted for those of the recurrent parent. Anderson (1949) has discussed the role which introgression may play in the development of hybrid populations, and in their spread into new territory not occupied by either parent. Although the importance of introgression in speciation and evolution cannot yet be evaluated, its contribution as a source of genic variability within a species is obvious.

By introgression, varying amounts of *G. armourianum* germplasm could be incorporated into allopolyploids from the backcross progeny of the *hirsutum-armourianum* hexaploid. If these simultaneously or subsequently acquire genetic or cytological barriers, self-perpetuating strains or incipient species could be established. In the absence of such barriers, introgression would serve as the source

[4] Characters like glabrous leaf, tinged lint, the anthocyanin complex (petal spot, red filaments, red anther sacs) and modifications of leaf and boll shape have been recovered from *G. harknessii,* closely related to *G. armourianum.* Unpublished data of the author.

of increased variability within the species *G. hirsutum*.

Summary and Conclusions

Doubling of the chromosome number occurred spontaneously in a single flower of an F_1 hybrid of *G. davidsonii* × *G. anomalum*.

The plants obtained from seeds of the fertile boll gave rise to a fertile amphidiploid strain combining the characteristics of both parental species.

The incompatibility of the new amphidiploid with natural species satisfies one requirement for its perpetuation as a distinct species, namely that of genetic isolation.

The production of the new amphidiploid is significant not only because it demonstrates that doubling of the chromosome number is a feasible method of forming new species, but because its spontaneous mode of origin parallels that suggested for the origin of the cultivated American species.

Doubling of the chromosome number occurred in one flower of each of two F_1 hybrids of *G. hirsutum* × *G. armourianum*.

The chances of this amphidiploid to develop into a true-breeding hexaploid are reduced by its low initial fertility, and by its interfertility with *G. hirsutum*. The possibility that new *hirsutum* strains with characters of *armourianum* could be developed by introgression is discussed.

Acknowledgment

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HYBRIDIZATION IN THE ANNUAL SUNFLOWERS: *HELIANTHUS ANNUUS* × *H. DEBILIS* VAR. *CUCUMERIFOLIUS*[1]

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INTRODUCTION

In 1945 seeds of sunflowers from three localities in Texas were sent to the writer by E. Mortensen. When plants from these seeds were grown they were found to approach *H. debilis* var. *cucumerifolius* in many characters although on the whole they were nearer to *H. annuus* in appearance (fig. 1). Subsequently a large amount of herbarium material was studied and it was concluded that natural hybridization between these two species probably occurs in eastern Texas. Field work in Texas in 1949 verified this conclusion, and some observations on the variation of these two species with an analysis of both natural and artificial hybrids is presented in the following paper.

Helianthus annuus is a wide-spread weed in much of North America and is morphologically quite diverse. Preliminary remarks concerning its variability have already appeared (Heiser, 1949). Plants of *H. annuus* from eastern Texas are usually very distinctive. The lemon yellow rays, the deep irregular serration (fig. 3, e) and somewhat undulate margin of the leaf, the purple mottled stems, and a tendency to produce long lateral branches from the base of the plant rather effectively distinguish most eastern Texas populations of this species from populations of *H. annuus* occurring elsewhere, although these traits occasionally appear outside of eastern Texas. In addition, the eastern Texas plants of *H. annuus* generally have few rays, small disks and bracts, and small achenes. These three characteristics are also found in *H. annuus* in California where introgression from *H. Bolanderi* is known to occur (Heiser, 1949).

Helianthus annuus is very common in east central Texas, often occurring in large populations along roadsides and in abandoned fields except in regions of sandy soils. In northeastern Texas this sunflower is more scattered in its distribution and is generally confined to vacant lots about cities and towns. Details of its distribution in western Texas are not available. The distribution map (fig. 2) has been compiled from the writer's own collections and from specimens in the following herbaria: Gray Herbarium of Harvard University, New York Botanical Garden, Missouri Botanical Garden, Southern Methodist University, the University of Texas, and the United States National Herbarium.[2] Whether *H. annuus* was originally native to Texas or whether it was introduced by man is not known. However, its occurrence only about towns and roadsides in eastern Texas suggests introduction by man.

Both morphologically and genetically *Helianthus annuus* appears to be more closely related to *H. argophyllus* (Heiser, in press), a species restricted to sandy soils in southern coastal Texas, than it does to *H. debilis* var. *cucumerifolius*. However herbarium specimens of *H. annuus* from Texas have been identified at times as *H. debilis* var. *cucumerifolius*. Although in Texas the last two species approach one another in appearance they are readily separated by a number of characteristics. *Helianthus annuus* is al-

[1] This study was aided by grants from the Penrose Fund of the American Philosophical Society and the Graduate School of Indiana University.

[2] I should like to express my appreciation to the curators of these institutions for making their specimens available for study.

FIG. 1. Greenhouse plant of *Helianthus annuus*. Seed from Zavala Co., Texas.

ways much larger in all parts of the plant. The involucral bracts offer the readiest means of identification. In *H. annuus* these bracts are broad, generally over 4 mm., hispid on the margins, ovate or oblong in shape, and abruptly attenuate (fig. 4, a, e); in *H. debilis* var. *cucumerifolius* the bracts are narrower, glabrous on the margins, lanceolate in shape and gradually attenuate (fig. 4, c). The rays in *H. annuus* are lemon-yellow or orange-yellow in color, and generally long and

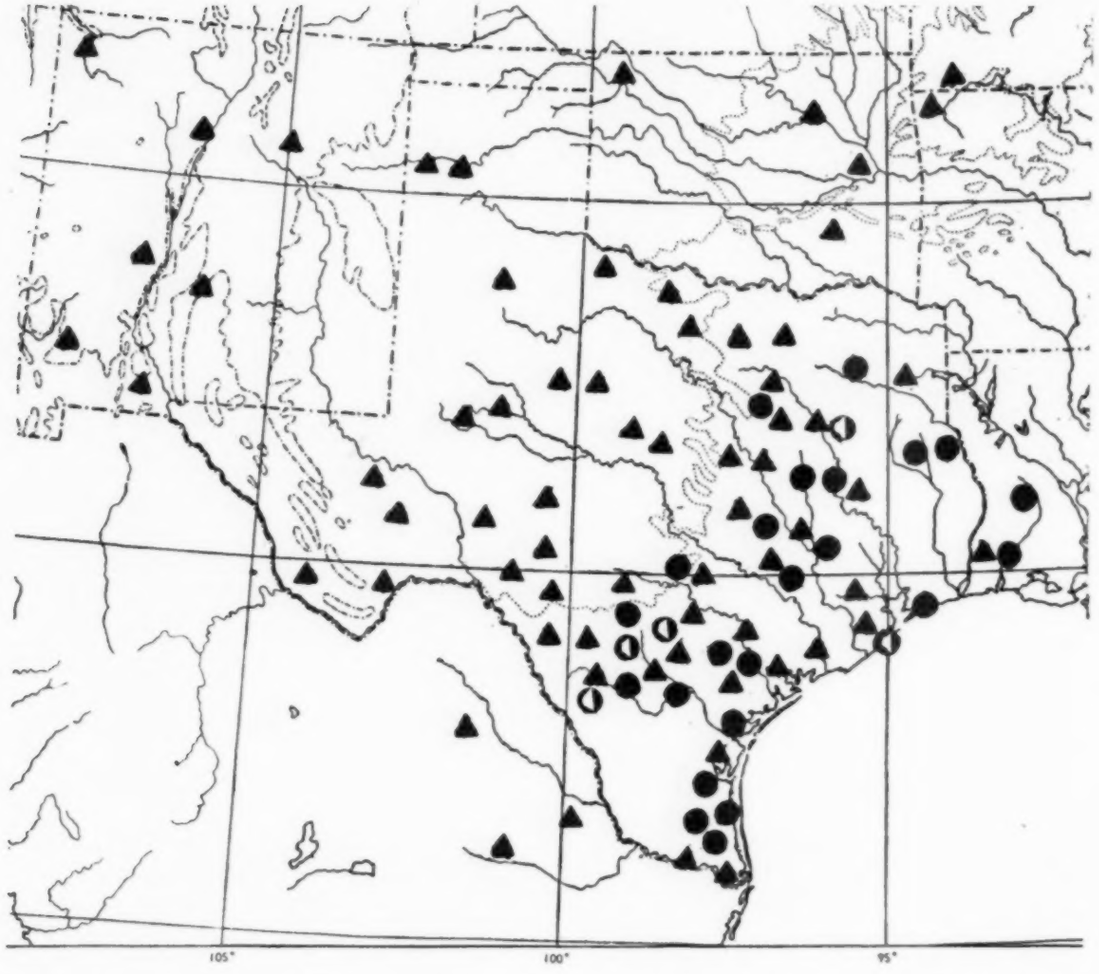

FIG. 2. Distribution of *H. annuus* (triangles), *H. debilis* var. *cucumerifolius* (black circles), and their natural hybrids (black circles with white designs) in Texas and vicinity. Base map used through the courtesy of Dr. R. E. Woodson, Jr. and the Missouri Botanical Garden.

narrow (with an index value-ratio of length to width of less than .40), whereas in *H. debilis* var. *cucumerifolius* the rays are a deep orange-yellow, and generally short and broad (usually with an index of over .40). The habitat difference is also striking, *H. annuus* seldom or never occurs on sand, whereas *H. debilis* var. *cucumerifolius* never occurs away from sand. There is a broad overlap in the time of blooming but in general *H. debilis* var. *cucumerifolius* comes into bloom in April whereas *H. annuus* rarely flowers before June. Both species have the haploid chromosome number of 17 (Heiser, 1948).

Without much doubt *H. debilis* var. *cucumerifolius* is native to Texas. Its distribution today is confined almost entirely to eastern Texas (fig. 2) and although it occurs as a roadside weed it is also found in undisturbed sites. Torrey and Gray (1841–43) originally described this entity as a distinct species, but Gray in 1884 considered it a variety of *H. debilis*. In a later treatment Watson (1929) again recognized the two as distinct species. *Helianthus debilis* var. *debilis* which is native to Florida and *H. debilis* var. *cucumerifolius* appear to be rather closely related from a morphological standpoint. It is proposed here to consider the Texas

material as a variety rather than as a species until additional study can be undertaken.

Within the assemblage of plants which we are calling *H. debilis* var. *cucumerifolius* there is considerable diversity. Forms from near Galveston, Texas, approach *H. debilis* var. *debilis* in appearance whereas forms from southern Texas approach *H. petiolaris,* a species which occurs on sandy soil in western and northern Texas and elsewhere in the western United States. *Helianthus debilis* var. *cucumerifolius* and *H. petiolaris* are allopatric in their distribution, and artificial hybrids between them show a high degree of sterility (Heiser, unpubl.).

The Two Species in Horticulture

Both *H. annuus* and *H. debilis* var. *cucumerifolius* are cultivated to some extent as ornamentals. Both species are

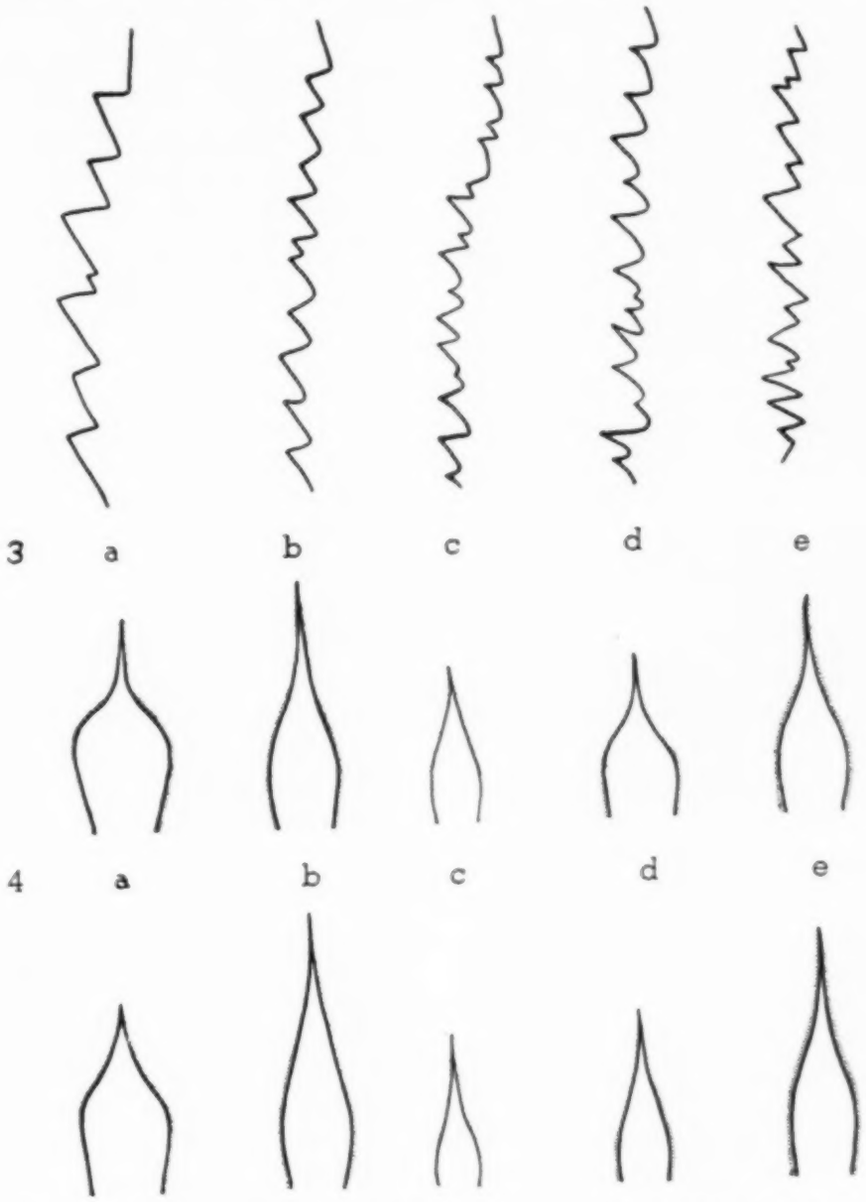

Fig. 3. Leaf serration. a. *Helianthus annuus* (St. Louis). b. *H. annuus* (St. Louis) × *H. debilis* var. *cucumerifolius.* c. *H. debilis* var. *cucumerifolius.* d. backcross (*4921*). e. *H. annuus* (Texas). × ½.

Fig. 4. Involucral bracts. Outer bracts above. Inner bracts below. a. *Helianthus annuus* (St. Louis). b. *H. annuus* (St. Louis) × *H. debilis* var. *cucumerifolius.* c. *H. debilis* var. *cucumerifolius.* d. backcross (*4921*). e. *H. annuus* (Texas). Slightly enlarged.

listed in the Burpee Seed Catalogue of 1889. Hence there has been ample time for considerable crossing between the two species in gardens. I have grown a number of ornamental strains of both species and it is apparent that some horticultural strains are the result of selection from hybrid derivatives of these two species. Hybrids between horticultural strains of the two species have been figured and described by Cockerell (1918, 1929).

When the present study was begun seeds of wild forms of *H. debilis* var. *cucumerifolius* were not available, and in the majority of the crosses to be described below a horticultural form of *H. debilis* var. *cucumerifolius* was used.

Artificial Hybrids

4922 [3]—*H. annuus* (St. Louis, Mo.) × *H. annuus* (Zavala Co., Texas) and reciprocal. The F_1 plants (18 in number) were intermediate morphologically between the two parents, extremely vigorous, and perfectly fertile. Examination of pollen mother cells showed 17 bivalents at metaphase.

4923—*H. annuus* (Zavala Co., Texas) × *H. debilis* var. *cucumerifolius* (Bodger Seed Co.) and reciprocal. The F_1 plants (7) were morphologically intermediate between the parents and were very similar to plants of *4921* (see below), although plants of *4923* could be distinguished from those of *4921* by the more pubescent edges of the involucral bracts. The F_1 plants were vigorous but highly sterile. The pollen fertilities ranged from 0 per cent to 9 per cent good pollen, with a mean of 3.6 per cent.

4843 and *4918*—*H. annuus* (St. Louis) × *H. debilis* var. *cucumerifolius* (Bodger Seed Co.) and reciprocal. These F_1 plants (17) were intermediate between the parental strains and were vigorous. Pollen fertilities ranged from 0 per cent to 22 per cent with a mean of 6.7 per cent. In the greenhouse these plants set no seeds when pollinated by *H. annuus*, but plants in the field set a few seeds when open pollinated and one controlled cross with *H. annuus* as the male parent yielded 12 seeds. Meiosis was studied in four plants, and the chromosome pairing was quite variable. The number of bivalents ranged from 5 to 15 per cell with a mean of 10.5 for the 70 cells studied. The remaining chromosomes were associated in one to four chains of from 3 to 8 chromosomes. Univalents were observed in over half of the cells. It is apparent then that the two parent species differ for several translocations. No evidence of inversions was seen. In general, the pairing in this interspecific hybrid is similar to that previously reported for *H. annuus* × *H. petiolaris* and for *H. annuus* × *H. Bolanderi* (Heiser, 1947, 1949).

4919c. Hybrid (*4843*) × *H. annuus* (St. Louis). The four plants, all vigorous, which were obtained from this backcross showed considerable diversity, but in general they more nearly approached the recurrent parent. The influence of *H. debilis* var. *cucumerifolius*, however, was quite evident in the shape of the involucral bracts. The pollen fertilities of the four plants were 5, 14, 50, and 67 per cent. Seed set on two of the plants with pollen from *H. annuus* was about 20 per cent, and a third cross failed to set seed.

4921—*H. debilis* var. *cucumerifolius* (Bodger Seed Co.) × hybrid (*4843*). Eight seedlings were obtained from this backcross, seven of which were vigorous and survived to maturity. One plant with a pollen fertility of 96 per cent was indistinguishable from the *H. debilis* var. *cucumerifolius* parent and may represent a self. The remaining plants were taller than *H. debilis* var. *cucumerifolius* and possessed a bract shape showing the influence of *H. annuus* and a lower ray index (.38) than is found in the H. *debilis* var. *cucumerifolius* parent. The leaf serration of three of the plants was more jagged than in either of the parents or in the F_1, and was similar to that of Texas *H. annuus* (fig. 3, d). These back-

[3] Herbarium specimens of the species and hybrids, bearing the numbers given here, have been preserved.

crosses otherwise resemble the F_1 combination *4923* (see above) except for the more glabrous edges of the bracts. Pollen fertilities on the backcrosses ranged from 3 to 49 per cent with a mean of 13 per cent. Over 50 per cent good seed resulted from one cross using *H. debilis* var. *cucumerifolius* as a male parent, although a second cross resulted in only 1 per cent seed set.

5012—H. debilis var. *cucumerifolius* (Georgia) × backcross (*4921–2*) and reciprocal. The 23 plants secured from these crosses were for the most part indistinguishable from *H. debilis* var. *cucumerifolius*, although on the whole the plants grew more rapidly and were slightly taller at maturity than is typical for this species. In addition, 16 plants had rays which were a yellow-orange rather than a deep yellow-orange color. Pollen fertilities ranged from 30 per cent to 97 per cent with a mean of 62 per cent. It should be pointed out that the *H. debilis* var. *cucumerifolius* strain used in this cross was from a different source than that used with other crosses, but it is essentially similar to the original strain and is completely fertile with it.

5014—H. annuus (St. Louis) × backcross (*4919c–1*) and reciprocal. The 8 plants of this population could not be distinguished from the *H. annuus* parent except for the slightly narrower involucral bracts. However, the plants were less vigorous than the parental type. The pollen fertilities varied from 40 per cent to 98 per cent with a mean of 72 per cent.

Records of seed set in *5012* and *5014* were not secured.

To summarize—(1) The fully fertile offspring of crosses between Texas and St. Louis strains of *H. annuus* indicates a close relationship in spite of the morphological differences between the parental types. (2) Hybrids between *H. debilis* var. *cucumerifolius* and two strains of *H. annuus* are highly sterile but a limited amount of good pollen is usually produced. (3) Plants of the first backcross generation involving the species hybrid are also rather highly sterile but as much as 67 per cent good pollen may be produced and as much as 50 per cent good seed may be secured. (4) Plants of the second backcross generation are practically indistinguishable from the recurrent parent, but show a reduction in fertility.

Natural Hybrids

Putative hybrids between the two species have been collected by the writer in five different counties in Texas (table 1, fig. 2). The hybrids generally occurred as one or a few plants, and appeared to be more stunted in growth than the parental species which were growing in the same vicinity.

There can be little doubt that these plants actually represent hybrids. The artificial F_1 hybrid between the two species had been grown before making the Texas trip, and the putative hybrids showed the same type of intermediate features. The hybrids of one collection (*3070a*) were recognized from a distance because of the intermediate color of their rays. The two putative parents were always found growing in the same vicinity with the supposed hybrids, either along roadsides or in vacant lots where disturbance of the habitat by man was obvious. When mature heads were present on the putative hybrids they were found to contain many undeveloped ovules. The

TABLE 1. *Natural hybrids between* H. annuus *and* H. debilis *var.* cucumerifolius

Collection number	Locality	Pollen fertilities of the individual plants
3045	vacant lot, Athens, Henderson Co.	2, 2, and 46%
3066	roadside, east of Carrizo Springs, Dimmit Co.	18, 25%
3070a	roadside between Moore and Devine, Frio Co.	6, 8%
3071	roadside, west of La Vernia, Bexar Co.	5%
3080	beach, Galveston Island, Galveston Co.	9, 18%
3081	roadside, Galveston Island, Galveston Co.	7, 10, 17, 25, 35, and 45%
3084	vacant lot, western edge of Galveston Island, Galveston Co.	11%

TABLE 2. *Ray number, disk diameter, and bract width in natural populations of* H. debilis *var.* cucumerifolius *in Texas*

Collection number	Locality	n	Number of rays		Disk diameter in cm.		Bract width in mm.	
			$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
3044	Henderson Co.	10	15.7	2.5	2.07	.16	2.1	0.1
3049	Houston Co.	10	19.0	1.9	2.24	.17	2.4	0.3
3064	Dimmit Co.	10	15.1	2.9	1.98	.13	2.4	0.2
3068	Frio Co.	9	18.3	3.6	2.01	.12	2.0	0.0
3070	Frio Co.	10	15.7	2.1	1.84	.19	2.0	0.3
3071	Bexar Co.	10	17.6	3.1	1.98	.12	2.3	0.4
3074	De Witt Co.	10	17.8	2.6	1.95	.15	2.0	0.3
3080	Galveston Co.	10	13.9	1.7	1.91	.19	2.5	0.2
3086	Nacogdoches Co.	10	13.7	1.6	1.62	.15	2.0	0.2
4365*	Willacy Co.	10	—	—	1.95	.02	2.6	0.5

* Collected by Robert Runyon.

amount of good pollen ranged from 2 per cent to 45 per cent (table 1) whereas pollen fertilities on the "pure" species gave counts of over 85 per cent good pollen. This great variation in the amount of good pollen in the hybrids may be due to the fact that only some of the plants represent F_1's and that others represent either backcrosses or F_2 progeny. As a result of detailed morphological study it would seem likely that the plants with the higher pollen counts (25 per cent and over) are backcrosses to *H. annuus*.

NATURAL POPULATIONS

The means and standard deviations of the number of ray flowers, disk diameter, and bract width are given for small local population samples of both species in tables 2 and 3. The mean ray number in all populations of *H. debilis* var. *cucumerifolius* is less than 20, whereas in *H. annuus,* with one exception, it is greater than 20. The mean disk diameter is less than 2.3 cm. in *H. debilis* var. *cucumerifolius;* in *H. annuus,* with one exception, it is greater than 2.5 cm. The mean bract width in *H. debilis* var. *cucumerifolius* is less than 2.7 mm.; again with the same exceptional population, it is greater than 4.2 mm. in *H. annuus.* Thus, with one exception, it is seen that there are clear cut distinctions in the

TABLE 3. *Ray number, disk diameter, and bract width in natural populations of* H. annuus *in Oklahoma and Texas*

Collection number	Locality	n	Number of rays		Disk diameter in cm.		Bract width in mm.	
			$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
3039	Pittsburg Co., Okla.	8	25.9	4.0	3.54	.50	7.3	1.5
3040	Collin Co., Texas	5	23.2	2.6	3.60	.09	8.0	1.6
3041	Collin Co.	5	21.4	1.5	3.40	.10	7.3	0.1
3054	Brazos Co.	10	21.3	2.3	3.54	.20	6.0	0.9
3058	Hays Co.	10	21.1	0.9	2.97	.22	5.5	0.2
3062	Uvalde Co.	10	20.6	1.6	2.99	.20	5.6	0.8
3065	Dimmit Co.	8	21.3	1.0	2.70	.16	4.6	0.6
3069	Frio Co.	5	20.4	0.6	2.58	.13	4.3	0.4
3073	Gonzales Co.	10	21.6	1.6	3.05	.12	6.0	0.6
3076	Victoria Co.	5	21.0	1.0	2.90	.25	4.7	0.3
3077	Matagorda Co.	10	21.2	1.5	2.85	.17	5.3	0.5
3079	Galveston Co.	12	17.3	2.0	2.30	.23	3.6	0.4
3082	Galveston Co.	5	21.2	1.1	2.64	.25	4.8	0.8
3083	Galveston Co.	5	22.0	1.6	3.28	.17	7.3	1.5
3085	Harris Co.	10	20.6	1.3	2.84	.18	4.6	0.6

means between these two species for these three characters.

The one exceptional population of *H. annuus* (*3079*, table 3) had a ray number within the range of *H. debilis* var. *cucumerifolius* but the bract width and disk diameter were outside the range of the latter species. In general appearance population *3079* resembled some of the artificial hybrid derivatives. However the plants were perfectly fertile, and hence do not appear to be first or second generation hybrids.

From table 3 it can also be seen that the Oklahoma population (*3039*) and the Collin County, Texas, populations (*3040*, *3041*) of *H. annuus* have the largest measurements in regard to the ray number, disk diameter, and bract width. These three populations are all north of the range of *H. debilis* var. *cucumerifolius*.

Discussion

The variation of *H. annuus* in eastern Texas is in the direction of *H. debilis* var. *cucumerifolius* in regard to the large proportion of leaves with jagged serration, speckled stems, small disk diameters, small achenes, low ray numbers, small bract widths, and the tendency to branch from the base. Measurements of ray number, disk diameter, and bract width of natural populations of *H. annuus* (table 3) have revealed that populations from outside of the range of *H. debilis* var. *cucumerifolius* have the larger measurements for these characters. Three possible hypotheses can account for the variation of *H. annuus* in the direction of *H. debilis* var. *cucumerifolius* in eastern Texas. (1) The forms of *H. annuus* which occur in eastern Texas are remnants of the ancestral population from which the two species have descended. (2) Parallel gene mutations have occurred in the two species under consideration and selection for these has resulted in forms which approach one another in certain morphological features. (3) The two species differentiated during isolation but complete genetic barriers between the two species were not formed. Through the agency of man *H. annuus* was brought into contact with *H. debilis* var. *cucumerifolius* and the resulting hybridization and backcrossing has introduced genes of *H. debilis* var. *cucumerifolius* into *H. annuus*. The crude methods of analysis available at present do not permit a positive choice of one of these.

However, hypothesis number one seems unlikely. First, it seems probable that *H. annuus* was introduced into Texas and was not native there. Secondly, *H. annuus* appears to be more closely related to *H. argophyllus* than to *H. debilis* var. *cucumerifolius*, and the latter is more closely related to *H. petiolaris* than to *H. annuus*. Furthermore if this hypothesis were true it would seem likely that *H. debilis* var. *cucumerifolius* arose through "ecological" rather than through "geographical speciation," which in itself would be difficult to explain (see Mayr, 1947).

The second hypothesis involving parallel gene mutations offers a more likely explanation and I am inclined to agree with Dobzhansky (1941) that some so-called examples of introgression might be just as readily explained on this basis. *Helianthus annuus* in Texas today is adapted to much the same climatic conditions as *H. debilis* var. *cucumerifolius*. If we assume that the characters of *H. debilis* var. *cucumerifolius* have survival significance in this region, then mutation in the newly introduced *H. annuus* in the direction of the native species might also have selective value in eastern Texas.

The third hypothesis merits particularly serious consideration in view of the fact that the two species hybridize natually and that forms resembling some of the presumed introgressants have appeared among the artificial hybrids. One serious drawback to the introgression hypothesis, however, is the high degree of sterility of the F_1 and the backcrosses. There would be a great selective disadvantage to the natural hybrids as a result of the sterility, unless the hybrid combinations had selective advantages to offset the ill effects of the partial sterility.

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Helianthus annuus when it was first introduced into eastern Texas (assuming that it was introduced) may have been poorly adapted and hence there might have been some selective premium placed on those hybrid forms which contained genes from *H. debilis* var. *cucumerifolius*, a species already well adapted to this area. Although the two species are now to some extent reproductively isolated, such may not have been the case when they originally came into contact. The partial sterility of the hybrids today may have developed as a challenge to hybridization as has been suggested by Dobzhansky (1941).

It seems likely then that gene flow into *H. annuus* from *H. debilis* var. *cucumerifolius* accounts for many of the peculiarities observed in eastern Texas populations of *H. annuus*. It is impossible to state whether or not there has been introgression in the reverse direction from *H. annuus* into *H. debilis* var. *cucumerifolius* because the latter entity does not occur outside of the range of *H. annuus* today and we have no "pure" populations available for comparison to give us some idea of its "normal" range of variation. From a study of ornamental varieties it is apparent, however, that introgression from *H. annuus* into *H. debilis* var. *cucumerifolius* has occurred in horticultural forms.

Although the two species hybridize it appears that some discontinuity between them has been preserved. If gene flow has occurred and *H. annuus* has been modified as a result, how has it been able to maintain itself as a distinct species in face of introgression from *H. debilis* var. *cucumerifolius?* The adaptation to different soils is probably a potent factor (Anderson, 1948) which in itself might help to preserve the morphological constancy, assuming that the physiological characters which adapt the plants to the different habitats are associated with morphological characters. Secondly, the sterility of the hybrids is so great today that the hybrid types are at a definite reproductive disadvantage. A slight difference in time of blooming also helps restrict genic exchange between the two species. These barriers in combination keep the two species distinct in spite of the hybridization which may have occurred in the past and which is occurring today.

One final problem confronts us: Should the eastern Texas populations be dignified with a Latin name? Single herbarium specimens of the Texas sunflowers are often difficult to distinguish from the sunflower of other regions. Only one population (*3079*) from Texas seems different enough from the remainder of the species that some taxonomists might prefer to give it subspecific status. *Helianthus annuus* is an ecospecies made up of many races or ecotypes. However, if all of the minor races of *H. annuus* were to be given names it would soon result in an unwieldly nomenclature. Introgression presents many taxonomic problems, and at present no nomenclatorial device is adequate to express the relationship thought to be involved. It may, of course, eventually be desirable to designate the Texas *H. annuus* population as a geographical race or subspecies, but the final solution must await more complete knowledge of *H. annuus* throughout its entire range.

Summary

Helianthus annuus in eastern Texas, where it was in all probability introduced by man, differs markedly from this species elsewhere throughout its range. The variation in a number of characteristics in the eastern Texas plants is in the direction of *H. debilis* var. *cucumerifolius*, which is native to eastern Texas. Artificial hybrids between the two species are rather highly sterile but produce some good pollen and seed. First and second backcross generations have been grown, and in the second backcross generation the plants are practically indistinguishable from the parent species although not so highly fertile. Putative natural hybrids

between the two species, which match rather closely some of the artificial hybrids, have been collected in Texas. In an analysis of ray number, bract width, and disk diameter of natural populations of the two species it is shown that there are generally clear-cut differences for these characteristics between the two species, although *H. annuus* approaches *H. debilis* var. *cucumerifolius* within the range of the latter species. Three possible hypotheses are entertained to account for the similarity of *H. annuus* to *H. debilis* var. *cucumerifolius* in eastern Texas. It is concluded that hybridization followed by introgression offers the most likely explanation, although the occurrence of parallel gene mutations cannot be entirely ruled out. The two species are able to preserve their morphological constancy because of different habitat preferences, a high degree of sterility in the hybrids, and a slight difference in time of blooming.

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EVIDENCE FOR INTERSECTIONAL FIELD HYBRIDS IN *LIATRIS*

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INTRODUCTION

While it is generally considered that natural hybrids between species are rarely found in the field, references to them have become more frequent in taxonomic and cytotaxonomic literature. Not only do these examples refer to intergradations between species somewhat closely related but with increasing frequency to crosses which traverse sectional lines (Ownbey and Weber, 1945; Weber, 1946), and even generic barriers (Mangelsdorf and Reeves, 1938; Mangelsdorf, 1947; Stebbins et al., 1946; Sax, 1947). With further observations in other genera additional data may be accumulated to help understand the bewildering question of isolating mechanisms (Dobzhansky, 1941; Stebbins, 1942) and to question further whether hybridization has been important in the evolution of species. In the Compositae a comparatively large number of hybrids have been reported. Heiser (1949) prefers not to accept this as a mere accident of study in a very large family. He does suggest that possibly this introgression as well as polyploidy are in part responsible for its complexities.

The genus *Liatris* of the Compositae, occurring only as a perennial, has attained considerable diversity in the characters of the underground stem but probably the greatest diversity in those of the head. Very early Cassini (1823) had observed differences in the appearance of the pappus of genera and in 1827 he explained the separation of the genus *Suprago* from *Liatris* on the basis of the length of the barbules. Though only one genus is now recognized, two sections I Suprago and II Euliatris still are used in classification. In the former, the pappus is referred to as barbellate or nonplumose to the eye and, in the latter, as plumose. Further grouping of the species into six series will also be referred to here. Figure 1 will give a ready reference for these as well as the relationships of the hybrids to be discussed.

Hybrids between species of these two sections were observed as early as the beginning of the century.

I. Torrey and Gray (1841) had described a new species, *L. Boykinii*, from a collection by Dr. Boykin (NY (type), G, US) [1] from near Columbia, Georgia, referring to the pappus as being "plumose, more so than *L. tenuifolia*." There are also specimens by the same collector of *L. tenuifolia* Nutt. and *L. elegans* (L.) Michx., but without any notations. In 1900 R. M. Harper collected specimens No. 634 (G, NY, US) and No. 635 (NY, US) in Sumter County, Georgia. He called the former *L. tenuifolia* and noted on one sheet of the latter that the plants were intermediate between *L. tenuifolia* and *L. elegans*. By comparison with the specimens described as *L. Boykinii*, they are very similar. Though no living plants have been studied cytologically, Small's (1933) comment about the

[1] The herbaria from which specimens are cited will be referred to by the following abbreviations: C—Herbarium of Chicago Natural History Museum; G—Gray Herbarium; M—Missouri Botanical Garden Herbarium; Mc—Herbarium of University of Michigan; Mn—Herbarium of University of Minnesota; NY—New York Botanical Garden Herbarium; US—Herbarium of National Museum, Washington; W—Herbarium of University of Wisconsin. The author wishes to express her appreciation to the curators of these herbaria for providing florets of the specimens.

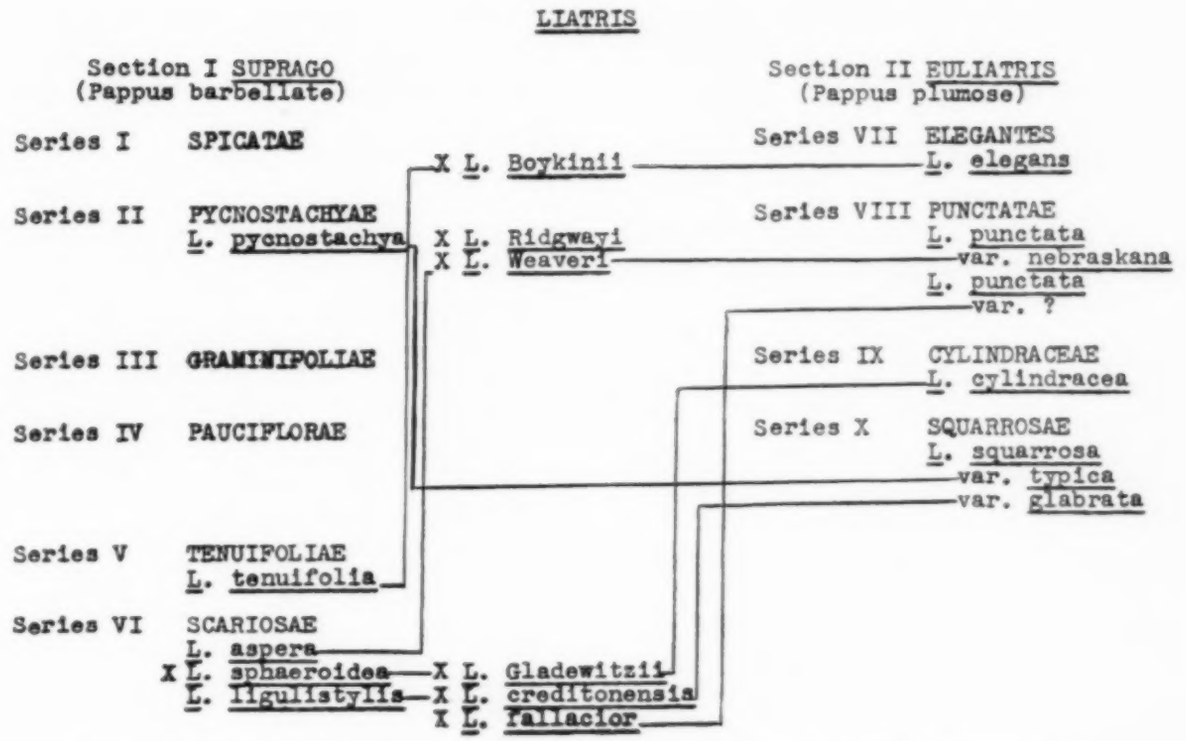

FIG. 1. Diagram showing the relationships of some species of *Liatris* between which putative hybrids are discussed.

species "perhaps a hybrid between *L. elegans* and *L. tenuifolia*" was believed to be valid (Gaiser, 1946).

This hybrid represents a cross between a species of the series Tenuifoliae of section Suprago and a species of the series Elegantes of section Euliatris. Five other intersectional hybrids involving species of at least three series of Suprago and each of the series of Euliatris have been recognized (see fig. 1). Though there are also interspecific crosses between species both within one series and of two different series, only those known between the two sections are dealt with at this time.

II. Farwell (1926) described his collection No. 7584, which had been found in an association of plants in Oakland County, Michigan, as a new species, *Laciniaria Gladewitzii*, stating it was "an exact intermediate between *L. cylindracea* and *L. scariosa* var. *sphaeroidea* and probably a hybrid of these." He called the pappus "very plumose." Though it has not been possible to examine the type at Cranbrook Institute, an isotype (Mc) has recently been received.

This hybrid is believed to have been found at least three times in as many different localities since then. Fassett's specimen No. 4478 (W) collected in Crawford County, Wisconsin, was recognized by Shinners (1943) as being the same hybrid. A second collection was made by Fassett, No. 15026 (W), in Kent County, Ontario, along the shore of Lake Erie. By recent communication it has been learned that he found only one plant there but that there had been two at the first location. Knowing that conditions similar to those along Lake Erie, existed along the southern shore of Lake Huron, the writer made a search for it there. In 1942 one plant was found on a sandhill in Lambton County, Ontario, where there were a few plants of *Liatris cylindracea* and a larger number of X *L. sphaeroidea* and *L. aspera* var. *intermedia* round about. From the examination of Farwell's specimens, recently received along with the isotype, it is evident that when he called *Laciniaria scariosa* var. *sphaeroidea* in the type description (No. 7587 Mc) is the same as X *Liatris*

sphaeroidea (Michx.) emend. Gaiser (1946). With more material accumulating, further discussion of the status of this and other interserial hybrids will be discussed at another time.

X *L. Gladewitzii* represents a hybrid between a member of the series Scariosae and the Cylindraceae of the two sections respectively.

III. Standley (1929) saw in a plant collected by R. Ridgway, No. 3265 (C (type) G, US) in Richland County, Illinois, and growing with *L. pycnostachya* Michx. and *L. squarrosa* (L.) Michx., a hybrid between the two. He described the pappus "about intermediate between the barbellate pappus of *L. pycnostachya* and the plumose pappus of *L. squarrosa*" and referred to it as "short plumose." It represents a cross between two polymorphic species of the series Pycnostachyae and Squarrosae each of different sections.

IV. Shinners (1943), when examining *Liatris* of the Scariosae complex, was keen to recognize evidence of hybridization in plants of Lunell's collections from Benson County, North Dakota. Lunell (1917) had described these as a new species *Laciniaria fallacior* from No. 1015 (Mn) and its variety *celosioides* from No. 1016 (Mn). The specimens combine characters of *Liatris ligulistylis* (Nels.) K. Sch., also of the series Scariosae, and *L. punctata* Hook. of the Punctatae, section Euliatris. This hybrid is known only from a type sheet consisting of two separate stems and an isotype of three stems.

V. Shinners (1943) also described the hybrid X *L. Weaveri* from specimens of plants No. 16, No. 17, and No. 7 plant 4 (No. 106365–4 (type), –5, –6 M) which had come from seed sent to the writer by Dr. E. J. Weaver from Lincoln, Nebraska, and grown at Crediton, Ontario. Gaiser (1951b) has compared the chromosomes of these plants, of some of the progeny of each, and of their putative parents which are taken to be *L. aspera* Michx. var. *typica* and *L. punctata* Hook. var. *nebraskana* Gaiser. This hybrid like the previous one involves a species of each of the two series Scariosae and Punctatae.

VI. A single plant of striking intermediacy between *L. ligulistylis* and *L. squarrosa* (L.) Michx. var. *glabrata* (Rydb.), which arose in the garden at the border of their adjoining plots, was described as the hybrid X *L. creditonensis* (Gaiser, 1946). Comparative studies of it and fifteen progeny resulting from open pollination have helped to establish its identity (Gaiser, 1951a).

In making a hybrid analysis according to Riley (1938) and Anderson (1949) use was made, along with other qualitative characters, of two measurable characters, namely the length of the barbules of the pappus and the abundance of pilosity on the corolla lobes. An intermediacy between the putative parents was found in the hybrid and an assortment in the progeny that suggested the possibility of back crossing to the *L. squarrosa* parent. In the measurements of the pappus barbules of the parental species, it was found that their means were quite different, with no overlapping at all of classes. The mean of the hybrid was equal to the extreme maximum of the barbellate parent. The barbule lengths of the progeny, with one exception, fell between those of the hybrid and the plumose parent. Thus a rather striking quantitative character was found which pertains not only to intergradation between two species but also to hybridization across the sectional line.

As can be seen from the foregoing report, three of the hybrids under discussion are known only from the herbarium specimens of the original collectors. Yet pappus and florets would be available from all of them. Therefore, it was decided to test them and their putative parents for the length of the barbules. Since those parental species included some from each series of the section Euliatris and at least three series of the section Suprago, measurements of a single species to represent each of the other series

of Suprago were also included. By random selection these were *L. spicata* (L.) Willd. of the Spicatae, *L. gracilis* Pursh of the Graminifoliae and *L. secunda* Elliott of the Pauciflorae.

Where, as in the case of X *L. Weaveri*, there were specimens of the progeny resulting from open pollination of each of the hybrid plants, a further analysis and comparison with results reported for those of X *L. creditonensis* was made. It was also possible in the several collections of X *L. Gladewitzii* and the three sheets of X *L. Ridgwayi* to score the pilosity of the corolla tubes in comparison with its abundance or absence in the putative parents. As this character pertains to only two of the hybrids it will be dealt with first.

Pilosity in the Corolla Tube

Ten specimens each of the putative parental species of X *L. Gladewitzii*, namely, *L. cylindracea* and X *L. sphaeroidea*, were scored for pilosity in the corolla basally (in the tube), medianly (in the throat) and terminally (in the limb). In the hybrid analysis of X *L. creditonensis* (Gaiser, 1951a) it was unnecessary to score for more than the last of these since the corolla of one of the parents, *L. liguli-stylis*, was entirely free of hairs. In that of the other parent pilosity was almost entirely limited to the lobes. However, since all the other species of the Scariosae have some pilosity in the closed part of the corolla, scoring for presence (+ to ++++) or absence (0) in the throat and tube had to be included here. The results are given in Table I.

Seven of the ten specimens of X *L. sphaeroidea* were so similar as to allow grouping under one score indicating heavy pilosity in the tube only. Two differed slightly in the amount of this pilosity and one showed a trace in the throat also. The ten specimens of *L. cylindracea* were of the same score. With the commonly recognized hairy corolla lobes, their score is diametrically opposed to that of the X *L. sphaeroidea*. By comparison the four hybrids all showed different combinations of the two, varying only slightly from one another. It is of interest to note that when examining some recent collections made in western Michigan by C. H. Bazuin, one divergent specimen of *L. cylindracea* (No. 8266) with a low scoring of + in each region of the corolla was found. This specimen while differing slightly from some of the others could not be recognized as a hybrid for certain.

The three sheets of X *L. Ridgwayi* were compared only with specimens of the two species among which it was said to have been found, from the same locality in Illinois, and by the same collector, R. Ridgway. The scores from the three

Table I. *Pilosity in the corolla*

Hybrid	Putative parent		No. of specimens	In corolla limb	In corolla throat	In corolla tube
	Species	Series				
X *L. Gladewitzii*			Farwell No. 7584 (Mc)	+	+	++
			Farwell No. 4478 (W)	+	+	++
			Fassett No. 15026 (W)	++	+	++
			Gaiser No. 243 (G)	+	+	+
	L. cylindracea	Cylindraceae	10 specimens	+++	+	0
			1 "	+	+	0
	X *L. sphaeroidea*	Scariosae	7 "	0	0	++++
			2 "	0	0	+++
			1 "	0	+	++++
X *Ridgwayi*			Ridgway No. 3265 (C) type	−+	−+	+
			Ridgway No. 3265 (G)	−+	−+	+
			Ridgway No. 3265 (US)	−+	−+	+
	L. squarrosa var. *typica*	Squarrosae	Ridgway specimens	+++	−+	−+
	L. pycnostachya	Pycnostachyae	Ridgway "	0	0	0

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sheets of the hybrid were very similar and about intermediate between the dissimilar parents. For an occasional scattered hair the score −+ has been used.

Length of Barbules of the Pappus

As in the earlier report on X *L. creditonensis,* in order to obtain the mean value of the barbule length of a parent, ten different herbarium specimens of the species were used and always twenty-five measurements [2] were made. Thus for each species here reported, the mean has been calculated from a total of two hundred and fifty measurements. Similarly, for the sake of uniformity, of each sheet of a hybrid, there are again twenty-five measurements. As there was some doubt about the efficacy of using this number, a test case was made of X *L. Weaveri* and its progeny, by comparing one hundred measurements each with the first twenty-five made. The calculations of the means from the two sets of figures showed no significant differences except that the standard errors were higher with fewer measurements. Therefore, the means here given for the hybrids are from one hundred measurements in X *L. Weaveri* and from twenty-five in all others. In the case of X *L. Ridgwayi,* this included the separate recording of the type and two isotypes from the three herbaria, though they may be all of one plant since Standley when describing the new plant referred to "the type material consisting of the upper portion of a flowering plant." Likewise, the figures of X *L. fallacior* for each of the two stems on the type and the three stems on the isotype sheet are given separately since it cannot be said with certainty from how many plants they were taken.

It must be emphasized also that the barbules along any seta are not of even length. Thus for this study, where the interest is in the length rather than the amount of variation in the barbules of each specimen, only the longer ones which caught the eye were measured. The figures given therefore in no way represent the range of variation in length but rather the upper limits for each species or hybrid examined.

In Table II-A are given first the calculated means and standard errors of barbule length thus obtained for the putative parents in the section Suprago, of each of these hybrids. The figures are all between twenty and thirty with the exception of *L. ligulistylis* which is less than a unit more. This aroused curiosity about the species of the other three series of the section. It is seen that those also fit into the same range, with that of *L. gracilis* of the Graminifoliae only a fraction under twenty. Thus, in the species examined, there is a striking similarity in actual measurement of these barbules of what has been called barbellate pappus. Of course, only half of the species of this section (8 of a total of 16) have here been measured.

To the right in Table II-C are given similarly means with standard errors of the barbule length of the parental species in section Euliatris. By contrast with those for species of section I the figures for II Euliatris barely more than cover the decade 90 to 100 (92.37 to 104.07). In this case, though but four species and a variety are included of the sixteen species of the section, there is representation of each of its four series. Thus the mean lengths of barbules in the pappus of species commonly called plumose was as surprising as that for the barbellate ones. When calculating the means of these with the longer barbules, it was noticed, however, that the number of classes was more numerous than in those having shorter barbules. Without giving all the statistics here, these comparisons can be seen clearly in the graph of frequency distribution (fig. 2). Small numbers of exceptionally long barbules were found in each example of the plumose but to the greatest number as well as of the greatest length in *L. squarrosa* var. *typica* (see

[2] Again measurements are given in ocular micrometer units for which by calculation of the microscope 1 unit = 5.2 μ.

TABLE II. *Means of maximum length of pappus barbules of intersectional hybrids*

A. Putative parents of Section I Suprago		B. Hybrids		C. Putative parents of Section II Euliatris	
I	*L. tenuifolia*	25.56 ± .1962	X *L. Boykinii*		*L. elegans*	97.18 ± .5251
			Dr. Boykin (G)	38.67 ± .8630		
			Harper No. 635 (US)	39.63 ± 1.1304		
II	X *L. sphaeroidea*	27.32 ± .2407	X *L. Gladewitzii*		*L. cylindracea*	98.52 ± .4659
			Farwell No. 7584 (Mc)	74.35 ± .5432		
			Fassett No. 15026 (W)	75.31 ± .8040		
			Fassett No. 4478 (W)	74.99 ± .8144		
			Gaiser No. 1191 (G)	56.11 ± .6588		
III	*L. pycnostachya*	23.05 ± .1941	X *L. Ridgwayi*		*L. squarrosa* var. *typica*	104.07 ± .5668
			Ridgway No. 3265 (C)	47.31 ± .9013		
			Ridgway No. 3265 (G)	46.57 ± .8120		
			Ridgway No. 3265 (US)	44.27 ± .8368		
IV	*L. ligulistylis*	30.54 ± .2820	X *fallacior*		*L. punctata* var. *nebraskana*	101.50 ± .4819
			Lunell No. 1015 (Type) (Mn)	60.91 ± .8784		
			Lunell No. 1015 (Type) (Mn)	65.55 ± 1.0568		
			Lunell No. 1015 (Isotype) (Mn)	62.03 ± 1.0664		
			Lunell No. 1015 (Isotype) (Mn)	63.79 ± .9848		
			Lunell No. 1015 (Isotype) (Mn)	67.63 ± 1.0760		
			Lunell No. 1016 (Type of var.) (Mn)	64.59 ± .9848		
V	*L. aspera* var. *typica*	28.51 ± .3222	X *L. Weaveri*		*L. punctata* var. *nebraskana*	101.50 ± .4819
			No. 16 Gaiser No. 200 (G)	43.23 ± .3080		
			No. 17 Gaiser No. 201 (G)	65.58 ± .4098		
			7 pl 4 Gaiser No. 1063656 (M)	67.23 ± .4923		
VI	*L. ligulistylis*	30.54 ± .2820	X *L. creditonensis*		*L. squarrosa* var. *glabrata*	92.37 ± .5235
			No. 52 Gaiser No. 617 (G)	43.85 ± .8708		

Additional species of Section Suprago

L. spicata	20.43 ± .0175
L. gracilis	19.83 ± .0223
L. secunda	21.85 ± .0161

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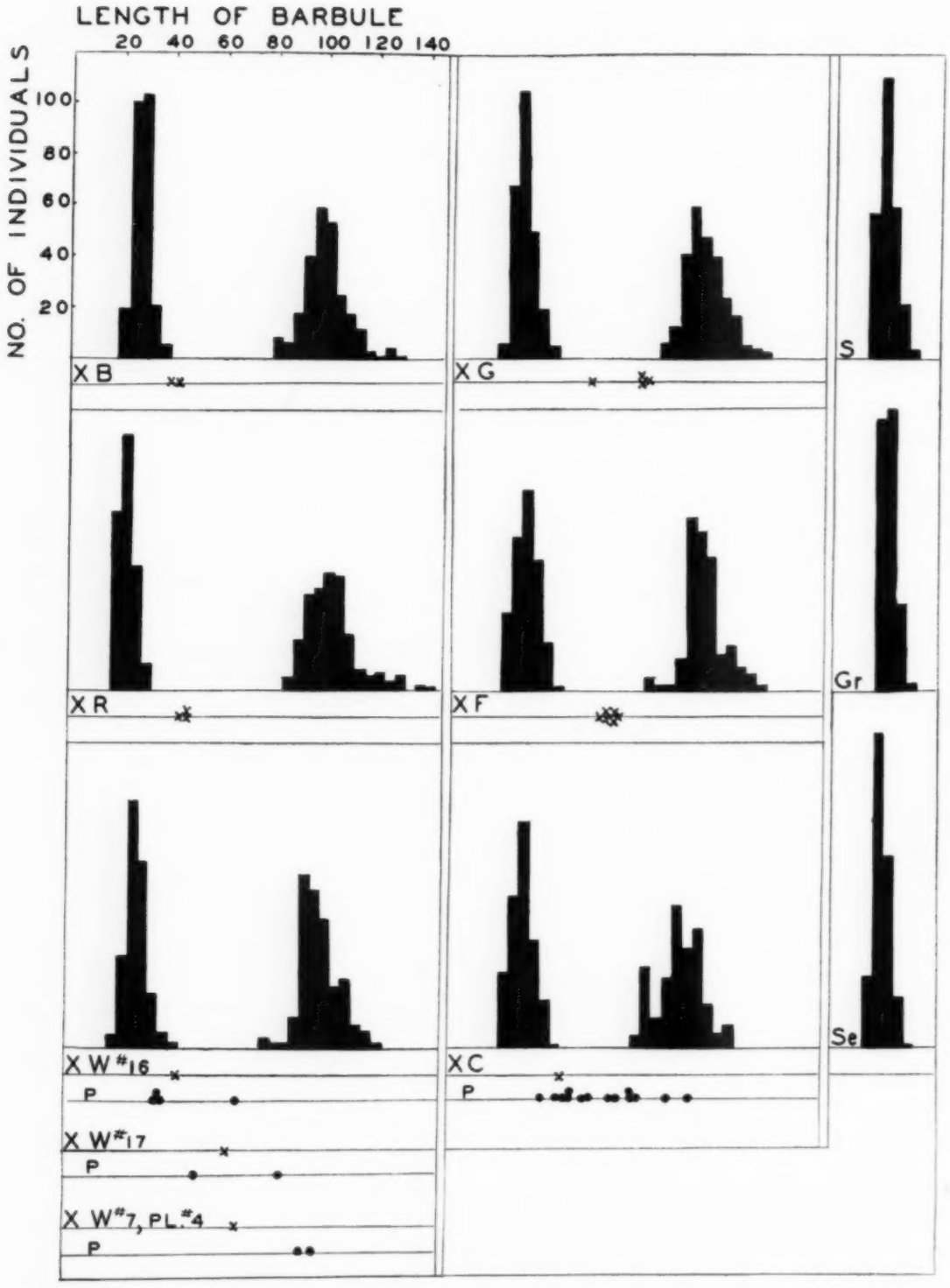

FIG. 2. Frequency distribution for the maximum length of barbules of putative parent species (Section I *Suprago* to left, Section II *Euliatris* to right) of intersectional hybrids of *Liatris* with the position of the means of the hybrids shown on a basal line. XB—X *L. Boykinii, L. tenuifolia* (left), *L. elegans* (right). XG—X *L. Gladewitzii,* X *L. sphaeroidea, L. cylindracea.* XR—X *L. Ridgwayi, L. pycnostachya, L. squarrosa* var. *typica.* XF—X *L. fallacior, L. ligulistylis, L. punctata* var. *nebraskana.* XW—X *L. Weaveri, L. aspera* var. *typica, L. punctata* var. *nebraskana,* with individul plants No. 16, No. 17 and No. 7 plant 4 and their progeny (P) on respectively lower lines. XC—*L. creditonensis, L. ligulistylis, L. squarrosa* var. *glabrata* with progeny (P) on lower line. S—*L. spicata.* Gr—*L. gracilis.* Se—*L. secunda.*

fig. 2 XR). This greater spread of exceptional classes undoubtedly explains the rather higher standard errors for these means than for those of the barbellate examples.

Medianly in table II-B are given the means and standard errors, calculated as explained, for each hybrid specimen. A close agreement of the three sheets of X *L. Ridgwayi* was to be expected since it was likely, from the type description, that they were all flowering stems of one plant. Similarly the figures of the six stems of X *L. fallacior* are fairly consistent though in this case there were at least two different plants (No. 1015 and No. 1016). There may have been three or even six depending upon whether the two stems on the type and the three on the isotype sheet were just from two different plants or each stem came from an individual plant. With the exception of these two hybrids, each figure given does represent a distinctly different plant. The two collections of X *L. Boykinii* are very similar. Only one of the four specimens of X *L. Gladewitzii* diverges much from the other three as does also one of the three of X *L. Weaveri*. It will be seen that the means of the hybrids are all intermediate between those of the two groups of parental species. The figures for all their means vary from 38.67 to 75.31, a range of over 35 units which is at least three times that of all species of either pappus type. The positions of their means in the bar graph (see fig. 2) shows that only those of two plants (X) fall within the marginal classes of the respective barbellate parent. These hybrids could certainly be called an intermediate group. Though a total of fourteen plants (considering the sheets of X *L. Ridgwayi* as one and X *L. fallacior* conservatively as three) is not large enough to be statistically significant perhaps, it represents all the specimens that have been seen. Their means are quite randomly distributed with about even numbers above and below an approximate mid-figure of 60.

Considering each hybrid from the above data, X *L. Boykinii* comes nearer the barbellate than plumose, as given by Torrey and Gray (l.c.). X *L. Ridgwayi* with a somewhat higher mean was called short plumose, but the mean, very like that of X *L. creditonensis*, is really closer to the barbellate. Since all the means of X *L. fallacior* are over 60, that hybrid is towards the plumose. One of the plants of X *L. Gladewitzii* is about equal to them, while the three others are much higher and most nearly approach the mean of the plumose parent of all the hybrids. Two of the three plants of X *L. Weaveri* (No. 17, No. 7 plant 4) are well over 65 and on the plumose side while No. 16 is only 43.23 and intermediate.

An interesting segregation is seen in the eight progeny of these three plants of X *L. Weaveri* in table III (see also fig. 2). The lowest mean was 34.23 and the highest 97.03, which represents a range of about 63 units, almost twice as wide as that shown in all of the fourteen hybrid plants. This in itself suggests backcrossing as was found in the fifteen progeny of X *L. creditonensis* (Gaiser, 1951a). In that population their range was from 35.85 (the only figure lower than the mean of the hybrid) to 94.05. Analyzed more carefully, the means of the barbules of three of the four progeny of plant No. 16 showed lower figures than the hybrid, as might result from a back-cross to the

TABLE III. *Mean length of pappus barbules of progeny of intersectional hybrids*

X *L. Weaveri* No. 16			
Progeny:	pl 3	Gaiser 911 (G)	67.79 ± .5212
	pl 11	Gaiser 912 (G)	34.63 ± .3612
	pl 13	Gaiser 913 (G)	37.35 ± .4379
	pl 17	Gaiser 914 (G)	34.23 ± .4682
No. 17	pl 6	Gaiser 915 (G)	83.55 ± .6761
	pl 24	Gaiser 916 (G)	50.95 ± .6930
No. 7 pl 4	pl 5	Gaiser 917 (G)	92.15 ± .7401
		Gaiser 918 (G)	97.03 ± .5986
X *L. creditonensis* No. 52			
Progeny (as given in Gaiser, 1951a)			

barbellate parent *L. aspera*. In contrast the means of two of the progeny were much higher than their parent No. 7 plant 4 and fall within the range of the parent species with plumose pappus. This certainly suggests back crossing to the plumose parent *L. punctata*. Thus the evidence in X *L. Weaveri* is for backcrossing to both parents. However it is possible that an additional interpretation might be considered, as was also noted for X *L. creditonensis*. The F_1 plants were intermediate between the parental strains for a quantitative character and their progeny showed greater variability. From the small number of progeny it would be possible to assume four classes, two-thirds falling within the range of the parental strains. This might be interpreted as suggesting the result in an F_2 from the evolvement of two loci of equal and additive effect.

Cytology

From the cytological studies the chromosome number in *Liatris* species was found to be almost uniform ($n = 10$) (Gaiser, 1949, 1950a, b, MS in preparation). In such a genus interspecific hybridization might be expected more frequently. There are, however, several exceptions involving polyploidy ($n = 20$) and aneuploidy ($n = 11$) in species here given as putative parents for two of the hybrids.

L. punctata var. *typica* (see fig. 4A) is tetraploid over the greater part of its wide range from the prairie provinces of Canada southward along the mountains to New Mexico. Variety *mexicanum* which extends into northern Mexico is also tetraploid. The diploid variety *nebraskana*, of a more restricted range in the central plains states, was recognized as far north as South Dakota. This variety was studied cytologically from a packet of seed received from Nebraska at the same time as one of *L. aspera* which gave the hybrid X *L. Weaveri*. From the chromosome number found in those three plants and their progeny (Gaiser, 1951b) there seems little doubt that they arose from *L. punctata* with the diploid genom.

The *L. aspera* population from Nebraska consisted of both normal diploids ($n = 10$) and aneuploids ($n = 11$). This was the only time aneuploids were found in the study of *Liatris*. The fact that each of the three plants of X *L. Weaveri* had the same unusual haploid number of 11 gave support to their origin from the aneuploid form of this *L. aspera*. Most of the progeny resulting from open pollination had the same chromosome number. There were a few (3 of 14) with irregular meiosis and varying numbers of bivalents and univalents. Two of the progeny of this hybrid were found with $n = 10$. Since there had been both the normal diploid plants of *L. aspera* as well as of *L. punctata*, they could have been backcrosses to either species.

By comparison, the hybrid X *L. creditonensis* and at least six of the progeny which were examined, all had the diploid number (Gaiser, 1951a). The meiotic divisions were regular as in the putative parents *L. ligulistylis* and *L. squarrosa* var. *glabrata*. Though another accession of *L. lingulistylis* gave rise to a population in which asynapsis was prevalent (Gaiser, 1950c) that was in no way related to the origin of this hybrid.

No variation in the chromosome number and no irregularity in meiosis occurred in the one plant of X *L. Gladewitzii*, conditions not anticipated in view of its high degree of sterility. However, from the root-tips of the few viable seeds that were obtained, the regular somatic number ($2n = 20$) was found in three and the triploid number ($2n = 30$) in a fourth. This is also an unusual number for the genus. Only the regular diploid number had been found whenever accessions of the putative parents *L. cylindracea and* X *L. sphaeroidea* were examined (Gaiser, MS in prep.).

There has been no cytological study of X *L. fallacior*, the second hybrid involving *L. punctata*, since it is known only from herbarium specimens. It raises the

very interesting question as to whether the diploid or tetraploid variety of *L. punctata* contributed to its origin. That the hybrid was found in a region considered to be north of the general range of the diploid is against the probability (see fig. 4B). Finding only the tetraploid when examining three accessions from two southern counties of South Dakota (Gaiser, 1950b) also suggests its prevalence over the diploid even in that state. However, it is not impossible for the diploid to have extended its range into some parts of the North Dakota.

Discussion

Further support has been obtained for the taxonomic and cytological determinations of these intersectional hybrids from characters of a quantitative nature. Measurements were made of a one-celled character in the case of the pappus barbule, and of a multicellular though few-celled character, in scoring for the abundance of pilosity in the corolla. Rollins (1944) had found a difference in the form of the trichome in the two species of *Parthenium* commonly known as guayule and mariola between which he recognized hybrids. He made such a character "the primary basis for the determination of the hybrids." In subsequent studies (1945, 1949) further use was made of the trichome sizes and forms in detecting apomictically produced progeny with varying chromosome numbers and estimating amount of introgression. In that genus confirmation for the variation in the trichomes of field hybrids was obtained by resynthesis. Regardless of whether or not such intrinsic characters belong to the group which are regarded as neutral in the maintenance of isolation between species (Mayr, 1948) they are effectively useful for the strikingly sharp differentiation of the parental classes. This affords clear recognition of intermediacy between them which has accompanied hybridization in these genera at least.

With perhaps the one exception of X *L. Gladewitzii,* the *Liatris* hybrids resulting from such wide crosses seem to have been found very rarely. At most only a few plants of any one have been collected. Certainly in no case was the observation of a hybrid swarm in nature reported as for *Wyethia* (Weber, l.c.) or *Salvia* (Epling, 1948). Between species morphologically so divergent as to be placed in two different sections of a genus, the formation of strong genetic barriers would be expected (Babcock, 1947). Dobzhansky (1941) singled out geographical isolation as of a different class from all

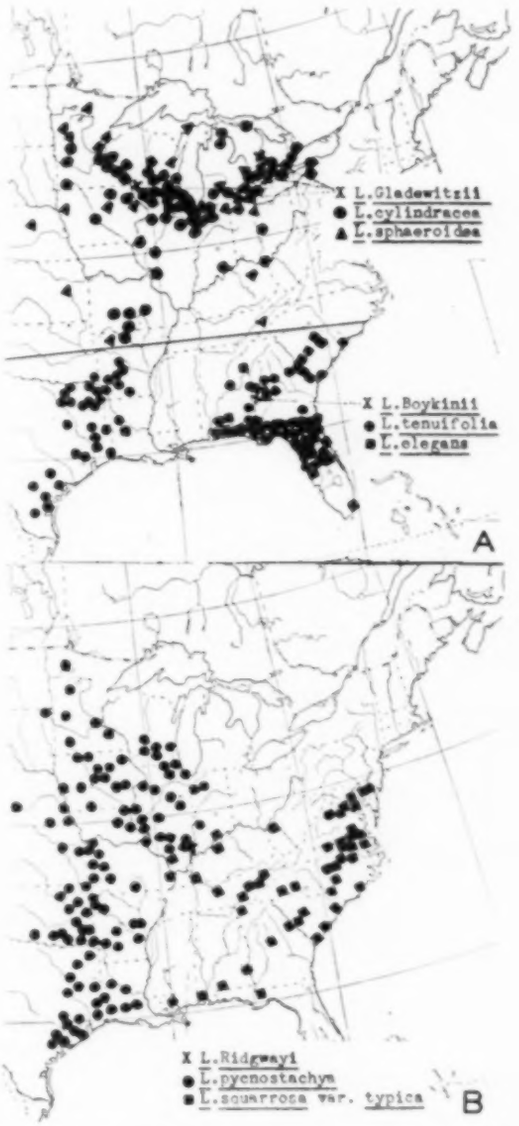

Fig. 3. Distribution maps of hybrids and their respective putative parents. A. (above) X *L. Gladewitzii,* (below) X *L. Boykinii,* and B. X *L. Ridgwayi.* Goode Base Map 102, used by permission of The University of Chicago Press.

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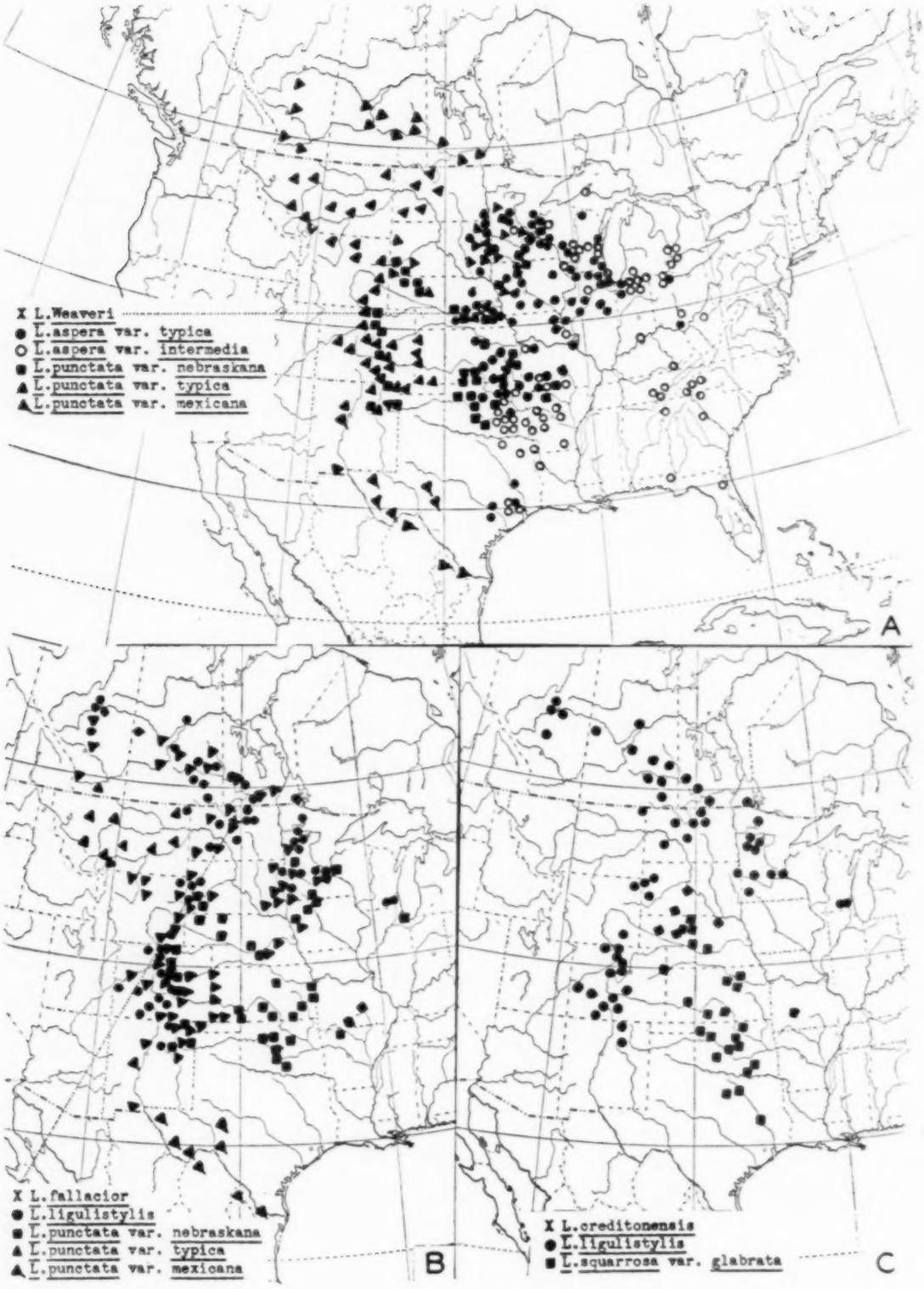

FIG. 4. Distribution maps of hybrids and their respective putative parents. A. X *L. Weaveri*, B. X *L. fallacior* and C. X *L. creditonensis*. Goode Base Map 102, used by permission of The University of Chicago Press.

isolating mechanisms but with the qualification that species may really be occupying separate areas due to certain physiological characteristics. To show how much the geographic ranges of the two parental species of each hybrid did or did not overlap, individual distribution maps [3] have been prepared in figures 3 and 4. Differing conditions are shown by the areas covered by each pair of parental species but with one exception they coincide in part at least. For X *L. Gladewitzii* (fig. 3A), which has been found more times than any other, there is practically complete coverage of the range of X *L. sphaeroidea* by the more widely distributed *L. cylindracea*. For X *L. Boykinii* (fig. 3A) there is also an almost equal coincidence over the range of the least widely distributed species although neither of the species is as widely distributed as some others. It is perhaps significant then that this hybrid was found by two different collectors. X *L. Ridgwayi* (fig. 3B) was found just about where the two populations meet. The source of X *L. Weaveri* is known as a region where both parents were cohabitant (fig. 4A). Only X *L. creditonensis* (fig. 4C), which arose in cultivation, seems to have come from species definitely isolated geographically. Since X *L. fallacior* could not be studied cytologically, the question of its origin from the diploid or tetraploid variety of *L. punctata* remains unanswered. The latter variety is coexistent with the other putative parent species *L. ligulistylis* which is diploid. Though the diploid *L. punctata* was not found quite as far north (fig. 4B) there may possibly be evidence for this in other herbaria.

Dobzhansky further subdivided the isolating mechanisms of parental forms that do and those that do not meet. In the latter categories are placed seasonal and ecological isolation. No particular seasonal variation in any parental pair of species has been found. Their concurrent blooming, as seen in the experimental plot, with those from the north earlier and those from the south later, would have created no isolation. The earlier blooming of the tetraploid variety of *L. punctata* (see Gaiser, 1950c, table I) would again favor the possibility of its cross fertilization with the equally early *L. ligulistylis* to form the hybrid X *L. fallacior*.

In considering ecological isolation it seems important to note that in the original descriptions of two of the hybrids under consideration, X *L. Ridgwayi* and X *L. Gladewitzii*, definite observations were reported of finding them along with both putative parents. For two others, X *L. Boykinii* and X *L. Weaveri*, the report might have been the same. No ecological preferences of the parents have been recognized. It is true that some species of *Liatris* do have very specific requirements of habitat such as exposed mountain sides or the Gulf coastal plain. However, from other collectors' notations and the author's observations made when collecting through the south central states, many do not require particular niches. Sometimes two of the species generally considered as having more divergent preferences were found at one stop, e.g. *L. spicata* var. *typica*, usually of wet lands, and *L. squarrosa* mostly of dry soils or, similarly, *L. pycnostachya* preferably of lowlands, and *L. elegans* of dry open wood lands. Several times *L. aspera* was found with *L. cylindracea*. Certainly a number of species show a wide tolerance. Also there is definitely no ecological isolation of the two sections. The only effective ecological barriers known to exist between two putative parent species here considered are those of the hybrid X *L. creditonensis*. *L. ligulistylis* prefers wet meadows, or land that is wet during at least part of the year in the north and in the

[3] The practice of representing one or more collections in any county, or approximately similar division in western Canada, by but one symbol has been followed here. Though additional specimens of more recent collections have been seen for some areas, for the sake of a more even representation only the specimens cited (Gaiser, 1946) have been mapped.

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mountains, and *L. squarrosa* var. *glabrata* occurs in the open dry plains to the south.

Yet despite the effects of the ecological as well as geographic isolation of these two species proximity of the two populations in the garden allowed gene exchange. This one exception among the *Liatris* hybrids bears a resemblance to the conditions found in *Balsamorhiza* (Ownbey & Weber, l.c.) where the interhybridizing species are so well separated ecologically as to rarely come into contact though they overlap in much of the area covered by the genus. In that genus the two sections are also separated ecologically as well as morphologically and yet a great number of intersectional hybrids were reported. This was spoken of as incomplete isolation with the production of segregating intermediates. Between species within each section there was complete isolation with and without the production of intermediates. In the genus *Wyethia*, Weber (l.c.) similarly found crosses taking place between various species of two of the sections when they came in contact though the sections were considered distinct morphologically and isolated by differences in habitat. As Huxley (1942) had generalized, Weber agreed that the changed conditions since man had utilized the natural range lands might have increased the opportunities for hybridization in *Wyethia*. There is certainly much in agreement with this and with the thesis, "hybridizing the habitat," of Anderson (1948) for X *L. creditonensis*. Also for it and for hybrids like X *L. Ridgwayi* and perhaps X *L. fallacior* where the two populations just meet there seems to be support for the deduction of Huxley (1942) "barriers will not tend to arise between closely related forms which have differentiated in separate geographical areas." Then the converse of his deduction "barriers will tend to be created between closely related species which show spatial overlap" would not be substantiated by the hybrids like X *L. Boykinii*, X *L. Gladewitzii* and X *L. Weaveri*. The distribution maps for them certainly show just that—spatial overlap. The appearance of hybrids from such species does not always seem to have been correlated with man-made disturbances either as Epling (l.c.) too found in *Salvia* hybrids.

For sympatric species, hybridization is chiefly excluded on the grounds of reproductive isolation. Two possible reasons why plant hybrids fail to perpetuate themselves are inviability and sterility. Concerning the first of these nothing can be said in regard to three of the hybrids since they are known only from the herbarium specimens and authors' descriptions. For each of the hybrids, X *L. Weaveri*, X *L. Gladewitzii* and X *L. creditonensis*, of which the writer had plants and seeds in varying quantities, the germination percentage of filled seeds was high (Gaiser, 1951a, b, MS in prep.). Thus from the observations in three of the six, inviability does not appear to give the explanation.

With regard to the question of sterility, the three hybrids varied. In one season, when seedlings were grown of the plant of X *L. creditonensis*, at least 259 filled seeds were recorded. Also the fifteen progeny studied were all fertile (Gaiser, 1951a). Of each of the three plants of X *L. Weaveri*, though the percentage of unfilled seeds was very high, the percentage of germination of filled seeds was approximately as high as that of *L. aspera* (Gaiser, 1951b, table I). Of their progeny, however, many set no seed and others very little. These two hybrids could be considered respectively as of high and low fertility, producing also progeny of varying fertility. By comparison, under the conditions in which it was grown, X *L. Gladewitzii* was distinctly a sterile hybrid. In four successive seasons for which it was examined the number of seeds collected were 9, 3, 0 and 0. However, caution must be exercised in such statements since one does not know all the factors conducive to fertility. It has already been noted from the hybrid analysis of the progeny result-

ing from open pollination of X *L. creditonensis* that they were considered to be largely back crosses to the one parent of which there were a considerable number of plants in the plot. Though a similar analysis was not made of the X *L. Weaveri* progeny, there were present many plants of both of the parents so that either back cross could have resulted. In agreement with this, the pappus barbules of over two thirds of the progeny fell within the two parental classes. This does support back crossing to both parents. For the one plant of X *L. Gladewitzii* only the one parent species *L. cylindracea* was grown along side of it and the numbers of it had become depleted latterly. Thus, there is no certainty that this hybrid could not have been fairly fertile if the other parent too had been in proximity.

While the reports of fertility and viability here given have been from conditions in the experimental plot which might have been varyingly beneficial or detrimental any one of these hybrids in the field would have had to compete with a large number of their parental species. As Epling (l.c.) pointed out not only would there be an abundance of parental pollen but the much greater number of parental seeds would naturally effect the chance for competing survivors.

Hybrids are believed to fail to perpetuate through selective elimination. The hybrids of two different species which occurred in two different habitats, not being as well adapted for either habitat as their parents, might be selectively eliminated. Thus, in *Tradescantia* (Anderson and Hubricht, 1938) and in *Iris* (Riley, 1938), intergradations were found only in the rarer intermediate zone and the disturbed areas respectively. Such selective elimination could be recognized where the two parent species were quite restricted to their particular sites. Where the two grow intermingled, as was noted to be the case in at least several of these *Liatris* hybrids, there seems less application for the theory.

Examination of the evidence here given shows that there is a strong tendency for short and long barbules in barbellate and plumose pappus of species. As shown in the graphs of those of the first section with barbellate pappus there is a striking overlapping. It is almost as remarkable in those of the second section with plumose pappus. While making measurements of several hundred specimens only one sheet (of *L. cylindracea*) was found to deviate much. Yet in six hybrids representing every one of the four series having plumose pappus with species of at least three of the series having barbellate pappus, the barbules are intermediate. No series, and so far not even a species, has been found to have barbules that fall into an intermediate place. Thus there has been a division of the genus morphologically into two groups of species which are not genetically isolated. Also there has been no geographical and no sharp ecological isolation of species of the two groups. The observation of the pappus of the progeny of these hybrids seems significant. In fifteen plants of the hybrid X *L. creditonensis* there was segregation for this one character from it toward the one parent. In eight plants of X *L. Weaveri* there was also segregation for this same character but two thirds of them fell within the two parent classes. Certainly that majority would be indistinguishable from the parents in this one character since they fell within the range of variation for the species. For this one character there seems good evidence for the failure to recognize perpetuation of a hybrid character. There is definite change from near intermediacy of the hybrids to a close approximation to the parents in the second generation by back-crossing. Of the fifteen progeny of X *L. creditonensis* resulting from open pollination the hybrid analysis confirmed the description of two as practically like the parent and eight very close to it. While the *Liatris* populations were not carried through further generations, it is suggestive of the findings in the genus

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Asclepias (Woodson, 1947). There very little external evidence of hybridity was seen in the progeny after the third backcross of the hybrid. The species of the two sections of *Liatris* remain discrete and morphologically distinct for the character of barbule length; at least no series with intermediate barbules has arisen and the two kinds have so far remained separated except for the occasional hybrid. This does not, however, exclude introgression. Since the one non-conforming specimen of *L. cylindracea* came from Michigan it might just possibly represent a backcross from X *L. Gladewitzii*. As Anderson (1949) has warned, we may be so impressed by the apparent evidence that hybridization is not occurring on a sufficiently large scale to have taxonomic consequences as to neglect the significant question of its possible genetic consequences. "A trickle of genes so slight as to be without any practical taxonomic result might still be many times more important than mutation in keeping up the basic variability of the parental species."

Summary

Six natural intersectional hybrids, earlier recognized taxonomically, were compared with their respective putative parental species in pappus and corolla characters. Comparison of pilosity in various parts of the corolla of two of the hybrids with their corresponding parental species confirmed the earlier observation in a third hybrid of their approximate intermediacy in this character. The barbules of pappus of the species of Section Suprago were clearly of a limited and overlapping range and those of Section Euliatris covered a different but almost equally limited range. Those of the hybrids were intermediate. For two of these hybrids it was possible to examine progeny resulting from open pollination. Those of one hybrid showed segregation suggesting back crossing to one parent and those of the other to both parents. Two thirds of the latter fell within the parental classes and thus within the range of variation of those species. Varying conditions of geographic, ecological and reproductive isolation obtain. The rarity of finding these hybrids and their failure to perpetuate cannot be attributed to any one cause. Undoubtedly there are a number of interacting influences. There is evidence, from the particular characters to which attention has been given here, of the quick masking of hybridization by back crossing.

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VARIATION AND ADAPTATION IN THE IMPORTED FIRE ANT

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INTRODUCTION

The South American fire ant *Solenopsis saevissima richteri* Forel is one of the insect pests which has become recently established in the Southeastern United States. In 1949 it was reported from Florida, Alabama, and Mississippi (Wilson and Eads, 1949). Its known distribution in these three states at that time is shown in Figure 1. Many other populations have been found during 1950 in Louisiana, Mississippi, Alabama, and Georgia by members of the Federal Bureau of Entomology and Plant Quarantine stationed at Mobile, Alabama (*in litt.*); these are mostly very young and limited to nurseries which receive shipments of plants from the Mobile area.

The first published record of this ant in the United States was made by W. S. Creighton (1930), who found it initially in urban Mobile in 1925. Creighton was told by H. P. Loding, a local and reliable amateur naturalist, that the ant had first appeared in the bayfront area of Mobile around 1918, had been pushed north of the city by the subsequently invading Argentine ant, *Iridomyrmex humilis*, and had later re-entered its original range. As late as 1928 Creighton found *richteri* still "confined to a comparatively small area extending from the northwestern part of the town to Spring Hill" (*in litt.*). In 1932 L. C. Murphree, scouting Argentine ants in Alabama, recorded *richteri* from several localities in Mobile and Baldwin Counties, including Whistler, St. Elmo, and Fairhope (Murphree, 1947).

The first comprehensive study of this ant was undertaken during the period of March to July, 1949, by Wilson and Eads (1949) under the auspices of the Alabama State Department of Conservation. The ant was shown to be a versatile but erratic pest, doing extensive damage to seeds and young seedlings of a variety of crops. Part of the data used in the following study was presented in that report. The U. S. Department of Agriculture initiated its own study in July, 1949, and has continued it up to the time of this writing (August, 1950).

During the spring survey of 1949 there was observed an unusual amount of variability in color from nest to nest. This variation included one extreme blackish phase referable to the typical subspecies *richteri*, one extreme reddish phase referable to no described form, and intermediates between the two. Furthermore, the phase referable to *richteri* appeared to be mostly limited to part of the periphery of the range (see fig. 4). Since Creighton in 1930 described the forms he found in Mobile as typical *richteri* and has later stated (*in litt.*) that this form was the predominant one during that early period, the possibility of the present predominance of the extreme reddish phase representing an important change in the population must be considered. The following report is an attempt to analyze and explain the variation in this light from the point of view of the entire population.

Most of the field data presented in this report was obtained during the 1949 survey. Experiments with living colonies and morphological studies were conducted during the following year at the University of Alabama.

Grateful acknowledgment is made to Mr. J. H. Eads for his invaluable collaboration in the first survey of the ant, to Dr. R. L. Chermock for continuous

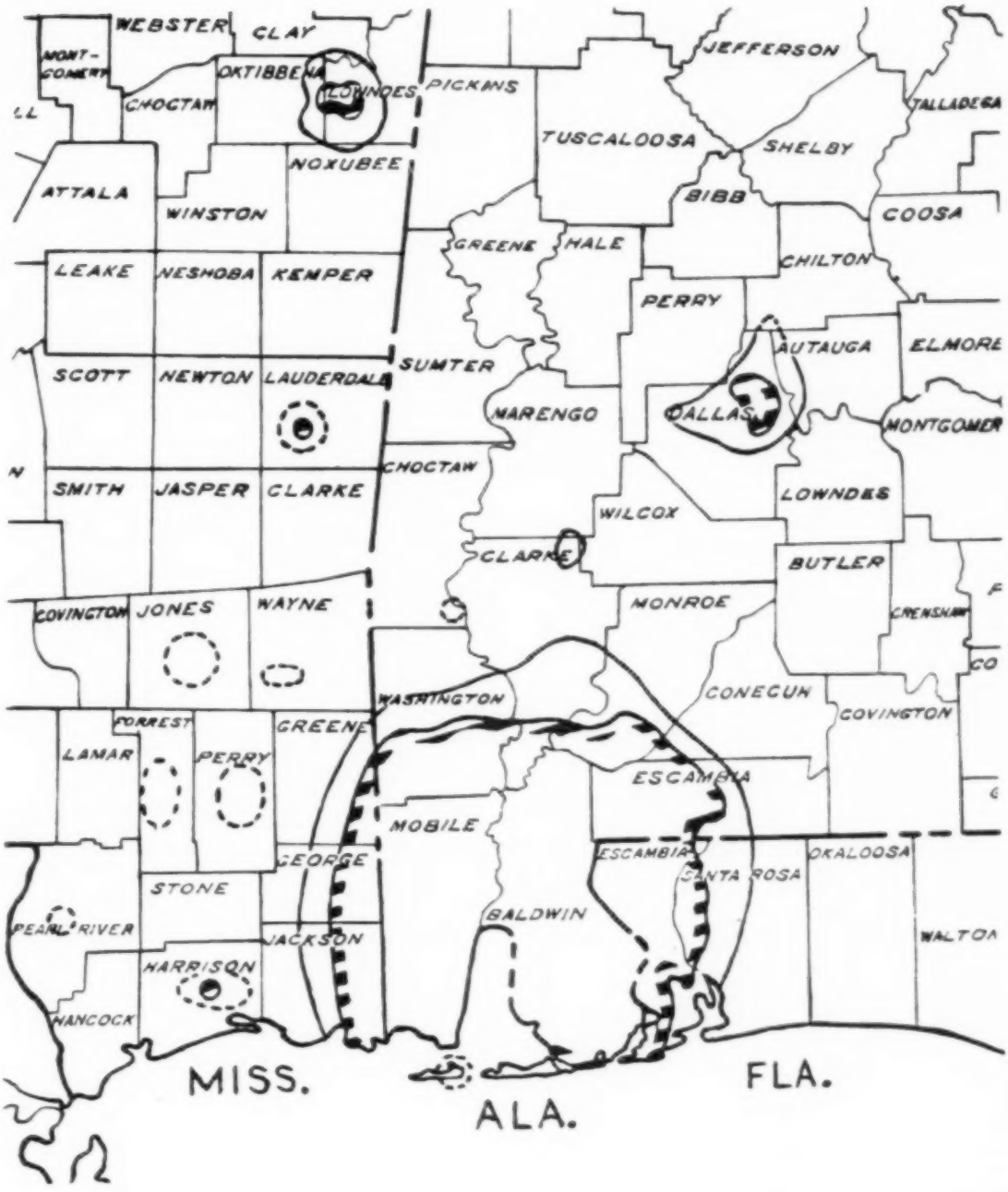

FIG. 1. Known range of the imported fire ant in the Gulf States in 1949. Inner barred lines enclose areas of heavy infestation; outer unbarred lines enclose the extreme range. Dotted circles indicate small populations the ranges of which were not accurately determined. The Choctaw County population and the populations in southern Mississippi were reported by the Federal survey crew (*in litt.*, 1949).

assistance and advice, and to Dr. W. S. Creighton for the hitherto unpublished information concerning the early infestation.

STUDY OF THE VARIATION

Solenopsis saevissima richteri Forel, as defined by W. S. Creighton in 1930, is apparently the southernmost race of a highly variable South American ant. Creighton described its range as extending from Uruguay south to the state of Rio Negro in Argentina, west to the Andes, and northwest almost to Bolivia. Another form, *S. saevissima* var. *quinquecuspis* Forel, is found over part of the range of *richteri* in eastern Argentina, but it has been distinguished from *rich-*

teri only on the basis of a highly variable color character and its validity is very questionable. *Solenopsis s. saevissima* (F. Smith), the typical subspecies, ranges with no great variability from the Guianas to the southern part of the state of Minas Geraes, Brazil. A vast zone of intergradation, containing a complexity of described forms, extends from Minas Geraes west through Bolivia to the Andes, south to Uruguay in the east, and south to the oases area of Argentina in the west. The taxonomic picture here is a very confused one; further study will probably reveal some of the forms to be intergrades of *saevissima* and *richteri*, while some may be shown to represent distinct species. A thorough discussion of the diagnostic characters and the known ranges of these forms has been presented by Creighton (1930). The extreme reddish phase, which plays so important a role in the Gulf States population, has not been formally described from South America, but it is possible that it exists there as a submerged element (see Discussion). The whole Gulf States population has been referred to in this report as *Solenopsis saevissima richteri* strictly as a matter of convenience. This has been its popular designation in reports and correspondence up to the present time. For reasons discussed later it is believed that the new form should not be given immediate formal taxonomic recognition.

The population found in the Gulf States exhibits a great deal of variation. In order to facilitate a more exact study, the extreme variants and their intermediates were divided into six arbitrary phases according to the color of the workers. These can be described as follows:

1. *Extreme dark.* Ground color of alitrunk and head piceous brown; a light brownish orange to light brownish fulvous stripe covering approximately the anterior three-fifths to four-fifths of the dorsum of the first gastric segment in all but the minimas and smallest medias; a similar stripe on the venter of the first gastric segment but the rest of the gaster piceous brown, the condition seen in all the phases. This is the form best referable to Forel's description of *richteri*.

2. *Dark intermediate.* Ground color of alitrunk and head dark brown but not piceous, and with no reddish tinge evident; stripe on dorsum of gaster similar to above.

3. *Intermediate.* Ground color dark reddish brown, lighter than dark intermediate phase and approximately intermediate between the two extreme phases; stripe on dorsum of gaster similar to two darker phases.

4. *Light intermediate.* Ground color medium reddish brown; stripe on gaster covering approximately one-half to two-thirds of the anterior surface, darker than in above phases, posterior border frequently indistinct.

5. *Dark red.* Ground color light reddish brown; stripe on dorsum of gaster covering approximately the same area as in light intermediate phase but darker, being very close to the color of the head and alitrunk and distinguishable only in contrast to the piceous brown of the rest of the gaster, its posterior border indistinct; stripe present only in larger medias and soldiers.

6. *Light red.* Ground color light reddish brown; stripe on gaster absent or present only in largest soldiers, very similar when present to that of dark red phase.

During the survey three colonies were found which could not correctly be assigned to any of the above phases. One of these, found near Gulf Shores, Baldwin Co., Ala., had workers with the ground color of the dark intermediate phase but with little or no gastric stripe. These are referable to Creighton's definition of *Solenopsis saevissima* var. *quinquecuspis* Forel (1930). The other two, found near Gulf Shores and Fairhope, Baldwin Co., Ala., had workers all of which possessed very nearly the same color as callows of the light red phase.

The queens of all the phases are very similar in coloration to the largest work-

ers and exhibit the same variation. The males are all uniformly black.

Morphological studies of the six phases revealed significant differences only in size. It was found that in workers, queens, and males, the darker phases are larger on the average than the lighter phases. As demonstrated in figures 2 and 3, the successive intermediates tend to show successive differences in size, this being particularly pronounced in the worker caste. All the measurements shown were made of the alitrunk as seen in profile, from the dorsal base of the pronotal collar to the dorsum of the junction of the propodeum and petiole. The alitrunk was used because of its rigidity and the ease with which it is measured. To correlate the variability of the head with that of the alitrunk, the heads in addition to the alitrunks of fifty light red workers and fifty extreme dark and dark intermediate workers were measured in profile from the base of the clypeal spines to the extreme occipital border. No significant divergence was noted in the two sets of measurements nor could the two groups of ants be separated on the basis of head-alitrunk proportion.

In nearly all the areas where many of the phases were observed together it was noted that the darker forms tend to build larger and proportionally taller mounds. Ten mounds each of light red and extreme dark-dark intermediate phases were measured in an open field several miles south of Theodore, Mobile Co., Ala., in June, 1949, and the following differences recorded:

Light red

The smallest mound had a base diameter of 13″ × 13″ and a height of 5″; the largest had a base diameter of 24″ × 22″ and a height of 11″. Height varied from 3″ to 13″. The overall average of the base diameters was approximately 24″ × 22″ and of the heights, 7″.

Extreme dark and dark intermediate

The smallest mound had a base diameter of 22″ × 20″ and a height of 10″; the largest had a base diameter of 39″ × 24″ and a height of 14″. Height varied from 10″ to 18″. The overall average of the base diameters was approximately 27″ × 24″ and of the heights, 14″.

All of the phases tend to accumulate bits of vegetable detritus, small pieces of charcoal, and small pebbles on the surfaces of their mounds, but this is especially noticeable in the darkest three or

	WORKERS	QUEENS	MALES
EXTREME DARK	1.264	2.682	
DARK INTERMEDIATE	1.236	2.635	2.712
INTERMEDIATE	1.130	2.584	
LIGHT INTERMEDIATE			
DARK RED	1.095	2.499	2.604
LIGHT RED	1.038		

FIG. 2. Means of the lengths in millimeters of the alitrunks of the color phases. For each phase a minimum of one hundred workers, twenty queens, and twenty males collected at two or more localities during at least two seasons were measured. Only statistically significant differences are shown.

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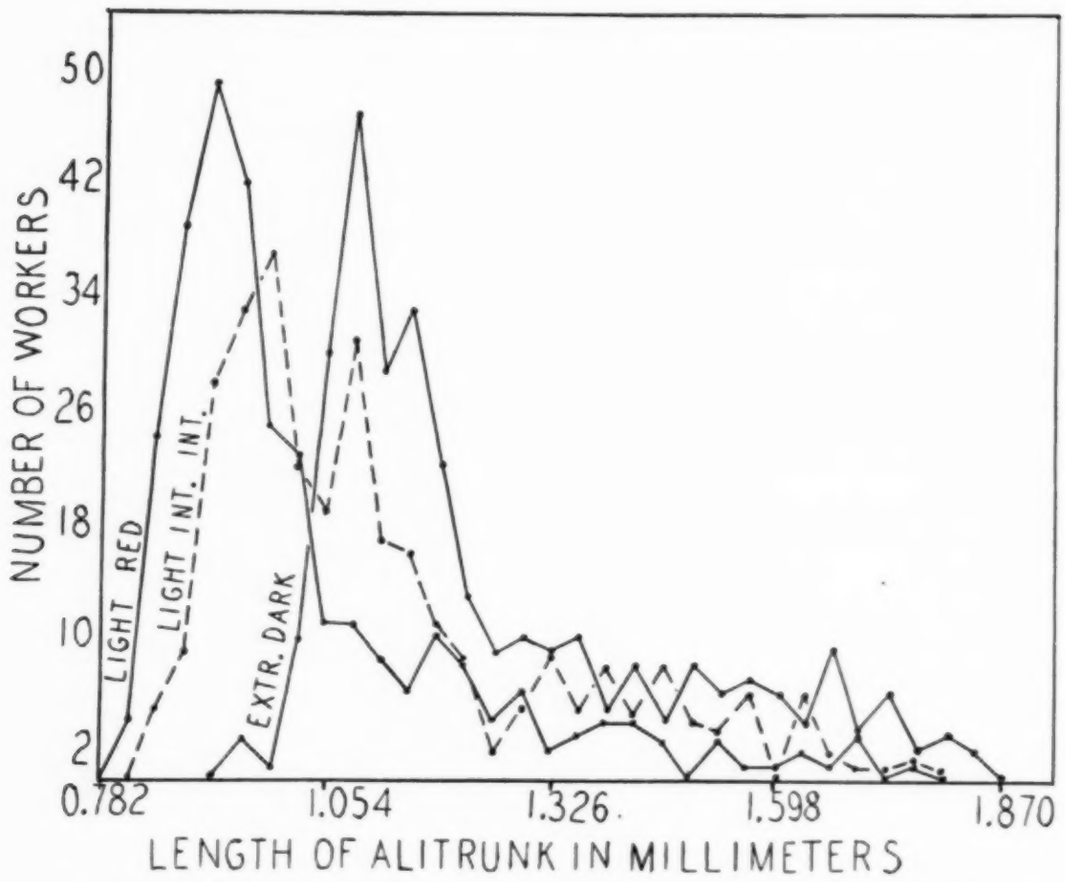

FIG. 3. The distribution of the workers according to size in the two extreme phases and two of the intermediate phases. Three hundred workers from four localities were measured in each group.

four phases. Occasionally mounds of the darkest phases are found nearly covered by a thin layer of this debris. In areas where they occur together it is often possible to tell with reasonable accuracy from a distance which are the darker and which are the lighter phase mounds, judging from the size, shape, and outer surface.

In order to plot the distribution of the color variants 10 colonies each in 84 relatively random localities over the main infested area were classified according to the six color phases. To supplement this a total of 193 colonies were classified in 18 other localities where ten nests could not be found together. Figure 4 shows the approximate distribution of the phases as determined by this survey. It will be noted at once that the darker phases are limited to the southern and eastern portions of the periphery of the range, to a small part of the western portion of the periphery, and to a number of small, isolated areas throughout the range. It is interesting to add here that the isolated areas are in nearly every case centered around marshy fields or grassland, but not all such situations contain darker phases. The Artesia and Meridian population in Mississippi are apparently homogeneously composed of the darkest one or two phases. In the Selma population the darker phases are scarce and irregularly distributed, and none at all have been found in the Thomasville population. The populations in Louisiana, Georgia, and southern Mississippi have not been carefully classified according to the color phases by the writer. However, Mr. G. H. Culpepper, of the Federal survey crew, has very kindly studied the color variation in these populations and has reported

that with the exception of the one at Meridian all contain a predominance of light phase colonies (*in litt.*). He has expressed the opinion that all but those at Meridian and New Iberia are apparently small and recent in origin.

It is believed that the variation studied in the Gulf States has a genetic basis. This conclusion is based on the following observations:

1. In many areas where both extreme phases and their intermediates occur, colonies of nearly all the phases may be found in the same immediate area, sometimes within a few feet of one another, apparently under nearly identical conditions.

2. Variation within individual colonies is very slight, and in none of the nests examined were there found workers which covered more than two adjacent phases.

3. It would be very difficult to rationalize the distribution of the variants according to environment or colony age. In the main area of infestation the darker forms are mostly limited to the southern and eastern portions of the periphery, while the population at Artesia, in northern Mississippi, is apparently composed entirely of darker forms. The Artesia and Selma populations are both located in the clearly defined "Black Belt," but the Selma population contains very predominantly the two lightest phases.

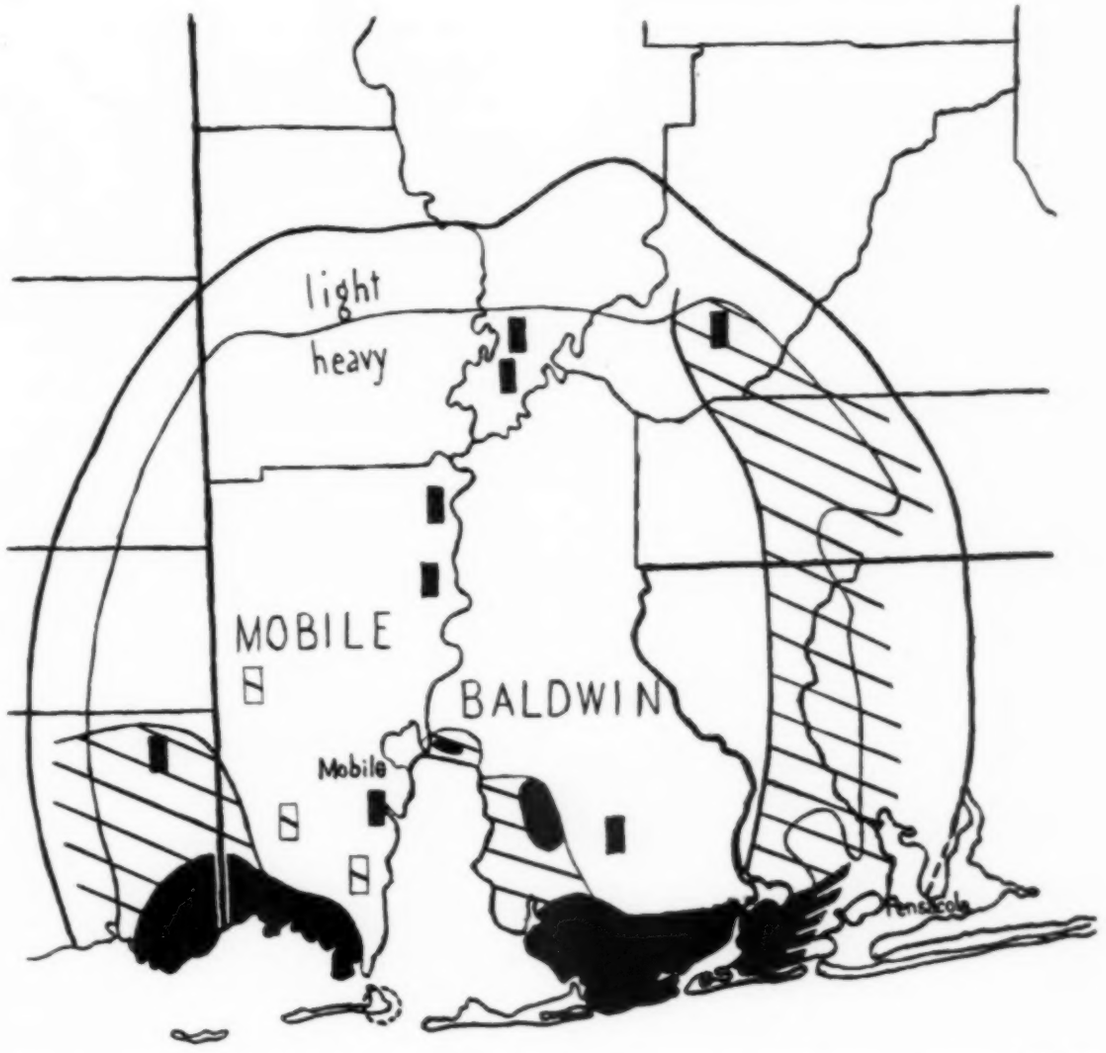

FIG. 4. Distribution of the color phases in the main area of infestation. Intense shading represents areas with incidence of four darkest phases greater than 20 per cent; hatching represents areas with incidence of these phases 5–20 per cent. Small rectangles represent small isolated dark phase populations.

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4. Colonies of light red and dark intermediate phases have been maintained in the laboratory under a variety of conditions without appreciable change in the color of the original workers or those reared in artificial nests. Workers have been reared at temperatures above 30° C and below 20° C; others have been heated excessively and chilled. Still others have been reared variously at substarvation and near-optimum conditions. Minima workers of the dark intermediate phase produced under substarvation conditions tend to be lighter in color but are still distinguishable from those of the lightest phases.

5. The brood of two light phase queens adopted by dark intermediate phase workers in the laboratory and one adopted by *Solenopsis geminata* workers developed into workers with the color of their mothers. In each case young, recently fecundated queens were introduced into groups of twenty to thirty workers. These were maintained in Fielde nests modified by the addition of plaster-of-paris chambers and were fed honey, dogfood, and miscellaneous insects. It has been found that occasionally groups of workers, especially those from depauperate colonies, accepted alien queens readily, but in the majority of cases could be induced to do so only after being chilled to immobility from several hours to several days. Many remained hostile regardless of treatment.

Discussion

It is apparent that the Gulf States population of *Solenopsis saevissima richteri* has undergone a marked change during the period of 1929 through 1949. The original population was at least mostly composed of the darkest phases, as stated by Creighton. As late as 1929 this remained true (Creighton, 1930 and *in litt.*). In 1932 L. C. Murphree collected the ant from five localities in Mobile and Baldwin Counties, Ala., and judging from his description (1947), the material he collected must be assigned to one or both of the two darkest phases. In 1941 the writer observed a large number of colonies along the bayfront of urban Mobile and in several areas in the western part of the city, all of which belonged to the lightest two or three phases. By 1949 the darkest phases could be found in some abundance only along part of the periphery in the main area of infestation and even there were outnumbered by the lightest phases. The Selma and Thomasville populations were predominantly light phase, the Meridian and Artesia populations at least predominantly dark.

Two approaches may be used to explain this peculiar recent distribution, one considering the history of the population, the other the possible climatic preferences of the extreme forms. Figure 5 shows the approximate rate and direction of spread of the ant since its introduction, as based on the observations of W. S. Creighton, the records of L. C. Murphree, and the estimates of 65 residents of the main infested area (Wilson and Eads, 1949). It appears that by 1934, while the dark phases may still have been dominant, the ant spread south over the southern portions of Mobile and Baldwin Counties, a range now co-occupied by another introduced ant, *Brachymyrmex heeri obscurior* Forel. Estimates place the origin of the Artesia population around 1935 and the Meridian population around 1940. The Selma population was not in any case estimated to have originated before 1944 nor the Thomasville population before 1948. The light phases were apparently responsible for the ant's explosive spread to the north in the main area of infestation. The partly peripheral distribution of the darkest, presumably oldest phases seems to indicate that they were pushed outward by the expanding light forms, in a pattern somewhat similar to that first demonstrated by Matthew (1939) for the primitive members of some groups of mammals, that is, with the most primitive forms at the periphery and the most recently evolved toward the center. The relatively homogeneous ecologi-

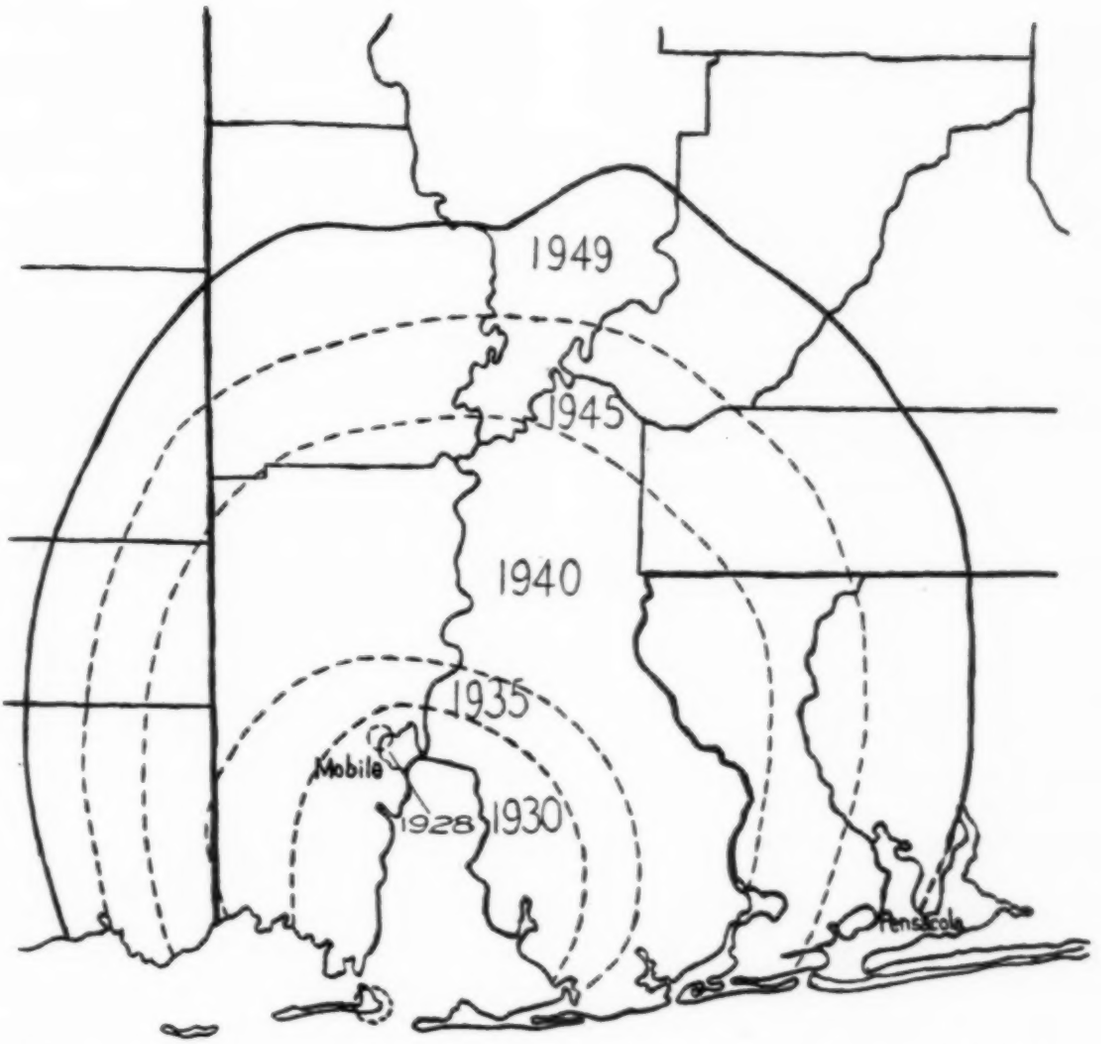

FIG. 5. Estimated rate and direction of spread of the imported fire ant in the main area of infestation.

cal conditions in and around the area of infestation, coupled with the absence of any significant geographical barriers, has allowed an even and steady spread of the ant since its introduction (see fig. 5). It has also resulted in the relatively clear preservation of the concentric pattern produced by the spread of the light forms. The darkest phases were best able to survive along the coast, along the eastern periphery, and in isolated spots through the infested area. Why marshy areas should suit these forms is not known. Large numbers of light phase nests often occur in the same places, with as many as seventy nests to an acre, and competition must be intense. Over much of the southern, continuous part of the range of the darkest phases, as around Gulf Shores, these forms occur in as wide a variety of situations as the lighter phases. The absence of light phases at Artesia and Meridian might be explained on the basis of early origin, that is, derivation from the early, nearly homogeneous stock. The lack of conspicuous success on the part of these populations, as compared with that of the younger Selma and Thomasville populations, and the southward expansion of the early population in the main area of infestation seem to indicate that the darker phases are poorly adapted to the climate of the Gulf States.

The present predominance of the light phases suggests an adaptive change within the population. The manner by which

these phases have largely replaced the dark phases has been, in the opinion of the writer, partly rapid expansion in range and population size and subsequent dilution of the dark phase genes, resulting in a diversity of intermediate forms; it has also been partly through considerable populational pressure and elimination in direct competition. An indication of this latter process can be seen in the scarcity of dark and intermediate phases over much of the range formally occupied by the dark phases. Another indication can be seen in the scarcity of the native fire ants, *Solenopsis xyloni* and *S. geminata*, and of the Florida harvesting ant, *Pogonomyrmex badius*, in the infested areas. Colonies of the imported fire ant are extremely antagonistic to these ants as well as to alien colonies of their own species. During the survey no colonies of *Solenopsis xyloni* and very few of *S. geminata* were found in the heavily infested areas. *Pogonomyrmex badius* was more common but quite sporadic in distribution. These three species reach relative abundance around the periphery of the imported fire ant's range. Another important consideration in this light is the incidence of the phases. Although exactly random samples in quadrats were not taken during the survey, approximately twice as many nests of the two darker phases were found as those of the two intermediate phases in the counts taken. Assuming that the phases represent nearly equal arbitrary divisions of the successive genotypes, it is possible that this difference in incidence is a result of replacement by the light forms through direct competition as opposed to genetic dilution. The relative importance of these two modes of replacement can only be estimated on the basis of available data, but it seems safe to say that both play an important role.

When considering the significance of the light phases as an adaptive replacement, the possible role of the Argentine ant, *Iridomyrmex humilis* (Mayr), must be studied. This ant reached its peak in the latter part of the 1920's and during that time succeeded in eliminating nearly all of the native ants in the Mobile area (Creighton, 1950). By 1932 it had been partly controlled and the native ants had begun to infiltrate the infested area. It was this time also that *Solenopsis saevissima richteri* began its initial spread to the south. It would seem quite possible that the decline of the Argentine ant, and not the replacement of the dark phases by the light phases, was responsible for the fire ant's rapid spread to pest proportions. However, several observations have been made which seem to indicate that the Argentine ant had a minor influence on the phenomenon under consideration. One is that the Argentine ant appears to offer the imported fire ant little serious competition at the present time, even in areas where the former are abundant enough to affect the native ants (Wilson and Eads, 1949). The two species thrive together in some areas of Mobile. Another is that the Argentine ant is primarily an urban dweller; it never was able to blanket the wide variety of rural situations in which the imported fire ant thrives (*Ibid.*). There is no reason why the fire ant could not have spread by way of these situations, even assuming that the Argentine ant was able to hamper it during that ant's peak. Finally, the predominantly dark phase Artesia population and the predominantly light phase Selma population can be critically compared, since both are under very similar conditions. The latter is less than half as old as the former and yet much larger and denser. Both are situated mostly in rural areas, and neither could have been greatly affected by the Argentine ant since their inception.

In considering the possible genetic basis of the variation, there are several peculiarities in the expression of the characters which deserve mention. One of these is the small amount of variability observed in intergrade colonies. This, coupled with the great variability existing from nest to nest, cannot be explained on

the basis of a single mutation. Admitting that the phases are totally arbitrary, that they overlap, and that occasional individuals can be assigned to an adjacent phase, at least four or five distinct genetic groups clearly exist; the workers of the six phases can be divided on the basis of size into five statistically significant units (fig. 2). Part of the difficulties are removed by explaining the variation on the basis of multiple factors or multiple alleles, which could control successional variation of the type observed. Of these two possibilities, multiple alleles seems to be the more tenable. From only three alleles a total of six combinations, or genotypes, is possible. Also, the greatest number of genotypes which could be produced by a single cross is three; the small amount of variability in single colonies studied in the field may well indicate such a limited number of genotypes. On the other hand, a dihybrid cross involving multiple factors showing no dominance would make possible nine genotypes and phenotypes, all of which, including the extremes, could be produced by a single heterozygous cross.

The close correlation between color and size variation and the present selective advantage the light phases hold seems to indicate a pleiotropic expression of whatever alleles are involved, producing a relatively clear-cut combination of characters for both extreme color forms. It would seem unlikely that these combinations of characters could maintain their identity in the extensive intergradation that has occurred unless they were very closely linked.

Even assuming multiple factors or multiple alleles, the small amount of variability within individual colonies is difficult to explain by the familiar laws of heredity. Provided that the queen is heterozygous and diploid, it would seem that the phenotypes of workers produced by an intermediate queen would be mixed according to random assortment. It appears very likely that the reason why this fails to occur in the imported fire ant (and in many other species of ants which exhibit the same peculiarity in their color varieties) entails an aberrant hereditary mechanism. One such possible mechanism is maternal determinism, a condition demonstrated in the snail *Limnaea peregra* by Diver, Boycott, and Garstang (1925). In this organism the direction of spiraling in the shell is determined by the genotype of the mother, regardless of the genotype of the offspring. On the other hand, in *Solenopsis* a mechanism involving haploidy in the queen and parthenogenesis is apparently rendered untenable, because unfertilized eggs are capable of developing at the most only to the late larval or pupal stage. Mature larvae were noted in fourteen out of fourteen nests containing only young alate queens; one of these nests produced several worker pupae, but since there was no absolute proof that all the queens were not fertilized, general conclusions concerning thelytoky should be avoided. One nest containing alate queens raised from larvae in the absence of males produced only larvae over a long period of time. This was noted in fourteen artificial nests out of fourteen which contained only virgin queens; mother queens in other nests kept up a prolific production of workers. Unfortunately, the interesting and significant problem of the genetic basis of the variation will prove to be a very difficult one to solve. For all practical purposes the colony is the individual in the life cycle of the ant, and with present knowledge of caste determination each generation of virgin queens will have to be preceded by hundreds or thousands of workers.

The origin of the light phases is another problem which can only be conjectured on the basis of available data. Three possibilities are treated below.

1. The light phases could have been a submerged recessive element in the genotype of the original invaders. However, this view is considerably weakened by the apparent homogeneity of the Artesia and Meridian populations, which were probably established while the dark phases

were still dominant. Also, the original invaders were probably few in number; it seems unlikely that they could have contained all the variability present today, unless this were to appear conspicuously in the early population.

2. The light phases could have been derived through mutations in the early, dark phase population. This possibility must always be considered, because the population mutation rate has been potentially tremendously high. Even in the early population, each of the many thousands of colonies were producing hundreds to thousands of sexual forms the year round. Today the number of colonies in the main infested area easily numbers into the millions (Wilson and Eads, 1949).

3. The light phases could have been derived from one or more later introductions. Despite the fact that nothing exactly comparable to the light red phase has ever been described, examination of representative material of most of the South American forms of *Solenopsis saevissima* has convinced the writer that the light red phase could have originated anywhere in the great zone of intergradation from southern Brazil to Argentina. Variation in this area is too great and as yet too poorly defined to dismiss the idea that the light phases were derived anywhere but in the Gulf States.

In final analysis the phenomenon can be described as an adaptive replacement, a shift in population dominance from one genetically distinct form (darkest phases, or *richteri* s. str.) to another (lightest phases). At present the population is quite unstable; it cannot be said to have reached an adaptive peak. Although it appears that a complete replacement is under way and a homogeneous population is in the making, new forms such as the two anomalous phases (see discussion of variation) may yet rise to dominance. The origin of the new form is not known. Because of this instability and uncertain origin, it does not seem wise to accord the light phases immediate formal taxonomic recognition, although by strict definition it might appear to some authorities to constitute a new subspecies. Otherwise, the question of the origin is an academic one only. Whether indigenous or introduced the light phases have functioned as a favorable mutation appearing in the population; they seem to have progressed very much as such a mutation would be expected to progress. As an example of this type of phenomenon the adaptive replacement in the Gulf States population is especially noteworthy. This is due to three significant conditions:

1. The new forms are easily identified and their history and present distribution can be carefully studied because of a distinct color character.

2. The adaptive change within the population has occurred so recently as to aid greatly the study of its history. The new forms constitute an almost vertical evolutionary change which has taken place in less than twenty years. Their history illustrates the extremely rapid rate with which such a change, which can be interpreted as an initial step in subspeciation, can occur in a population of insects. Similar changes have been observed in populations of the scale insects *Aonidiella aurantii*, *Coccus pseudomagnoliarum*, and *Sassieta oleae* (Quayle, 1938), and of the codling moth, *Carpocapsa pomonella* (Hough, 1934, and Boyce, 1935).

3. The very uniform terrain of the Gulf Coast area has allowed an identifiable preservation of what is apparently a concentric distribution of the old and new forms. That the dark forms have been pushed out along the periphery is still evident in their distribution today.

This populational change is indicative of the way that evolution can proceed in any population of ants. However, the rapidity with which this has occurred is probably rarely equaled by that in endemic species. Too little is known about North American ants at the present time to determine precisely the rates of evolution, but it appears that most holarctic genera have been evolving at a consid-

erably lower rate than such better known groups of insects as the Rhophalocera. For instance, postglacial relics are rare or absent, and subspeciation initiated by glacial isolation seems to have progressed to a relatively slight degree. The accelerated evolution in the imported fire ant probably has the same origin as the explosive spreads of imported insects as a whole: the removal of the biotic pressures (parasites, competition with other insects, etc.) which controlled it in its native environment. If this is true, then the populational change in the imported fire ant can be regarded only as a swiftly enacted replica of the normal evolutionary processes and not as typical subspeciation.

Summary

1. The imported fire ant, *Solenopsis saevissima richteri* Forel, is the southernmost race of a widespread and highly variable South American ant. It was introduced into the port of Mobile, Alabama, sometime around 1918 and by 1949 had spread to parts of Florida, Mississippi, and Louisiana.

2. A great deal of color variation from nest to nest has been noted in the Gulf States population. This includes an extreme blackish phase referable to the original description of *richteri*, an extreme reddish phase referable to no described form, and intermediates between the two. This color variation is correlated with differences in size of the ants and in appearance and proportion of their nests.

3. The variation has a genetic basis. It is suggested in this study that the variation can be explained most readily on the basis of multiple pleiotropic alleles.

4. The history of the variation has been determined as follows:

The darkest forms, or *richteri* s. str., were the ones originally dominant from the time of the ant's introduction until at least 1929 and probably sometime after 1932. The origin of the new form is not known, although it is believed that it originated either through mutation within the population or through a second introduction. In 1949 it was by far the dominant form. It had apparently replaced the typical *richteri* partly by rapid expansion and subsequent genetic dilution and partly through natural selection by direct competition. Its predominance in the main population and in at least two smaller isolated populations has evidently been responsible for a much greater success of the species. In the main population in 1949 the typical *richteri* was mostly limited in distribution to portions of the periphery of the range, forming with the new form roughly the concentric pattern of Matthew's modified Age-and-Area hypothesis.

5. The new form has been interpreted as functioning, regardless of its origin, as a favorable mutation introduced into the population. Its rise to dominance has constituted an extremely rapid, nearly vertical evolutionary change.

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NOTES AND COMMENTS

SEX-CHROMOSOME IN HONEY-BEE

WARWICK E. KERR

Since the first papers on the cytology of the honey-bee by Petrunkewitsch (1901), Meves (1907), Doncaster (1907) and especially Nachtsheim (1913) until that by Sanderson and Hall (1948) it has been generally accepted that *Apis mellifera* L. (honey-bee) had females with 32 chromosomes and males with 16. Recently F. J. Manning (1948–1950) described the discovery of a sex-chromosome and other important cytological details in *Apis*.

As this matter is of great importance, modifying the concepts of sex-determination in the honey-bee, we have prepared slides of testes of drones and found the following observations on the spermatogenesis of *Apis* by Manning to be correct: (a) there is a heteropycnotic chromosome; (b) this chromosome, called X-chromosome by Manning, does not go to the poles in the II meiotic division but is eliminated (fig. 1), and thus the spermatozoa have only 15 chromosomes; (c) in some phase of the maturation division chromosome counts show 8 or 9 chromosomes (in sections) and with acetic orcein smears it is easily seen that these chromosomes are at least double. Such pairing was earlier observed by Nachtsheim (1913), Doncaster (1907), and Meves (1907), but its occurrence was not found by Sanderson and Hall (1948).

Manning made two important statements regarding oogenesis: (a) he observed that the female has 31 chromosomes (and not 32 as believed before); (b) he originated the hypothesis that 4 nuclei are formed, two with 16 and two with 15 chromosomes, the latter becoming polar nuclei. These claims of Manning seem to us well conclusive. Regarding this cytological behavior one must assume that the sex in the honey-bee is determined by arrhenotoky plus a mechanism superimposed on it. If one assumes maleness of X-chromosome and femaleness of the autosomes, the sex in the honey-bee may be represented by a scheme of genic balance where X/15A is ♂, producing spermatozoa with 0/15A, and X/30A is ♀ producing eggs with X/15A.

It is interesting to note that such a mechanism permits the possibility of maternal inheritance, without recurring to cytoplasmic effects, because only females transmit X-chromosomes to both sons and daughters, while the males lose them in the second spermatocyte division.

We think that the failure of earlier investigators to observe the X-chromosome was a consequence of considering any cytological abnormality resulting from alterations of temperature. Thus the X-chromosome may actually have been seen, but was classified together with real abnormalities.

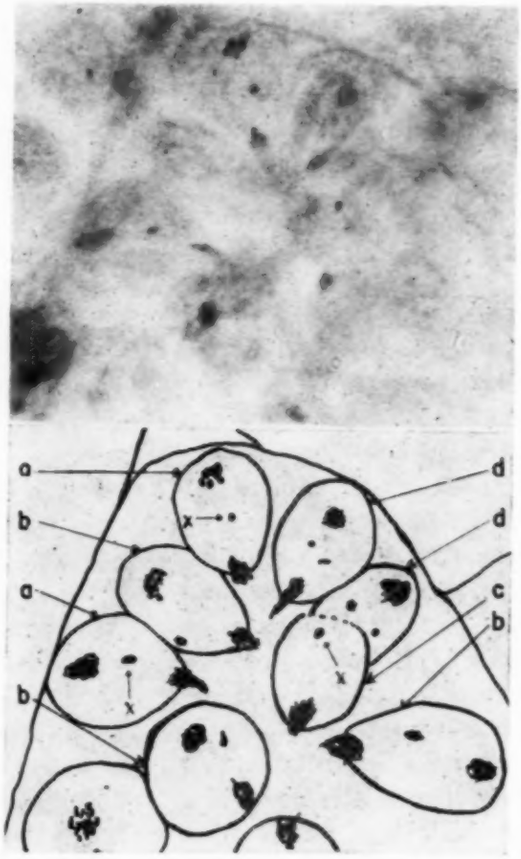

FIG. 1. Elimination of the X-chromosome in *Apis mellifera* L.

Telophase II in spermatocytes of *Apis mellifera* L. showing the extrusion of one nucleated bud and the elimination of the X-chromosome (Sections with 12μ, stained with Heidenhain's Iron Hematoxylin). The drawing was made on a photocopy, which was then dissolved; details not visible in the photo were added in accordance with direct observations in the microscope. Cells visible in the microphoto are lettered *a;* in these two cells and in the cells with letters *b* and *c* the X-chromosomes do not go to the poles, but remain in the equator as a diad. The cell *c* was cut and its second pole was in the next section. In the two cells *d* the X-chromosome is divided, but both daughter chromosomes remain in the equator, and do not enter in the spermatid nucleus.

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PRINCIPLES OF ANIMAL ECOLOGY [1]

FRANK A. PITELKA

This important compendium of ecological principles, generously documented, is divided into five parts: history of ecology, analysis of the environment, populations, communities, and evolution. The book is well illustrated, well indexed, and excellent in format. It contains an exceptionally useful bibliography of 71 pages. The scope of the work which the authors undertook is truly impressive, and the result stands without equal as a summation of ecological knowledge.

By now this book has been reviewed in several different journals, and no additional description of it seems necessary. In an earlier review (Auk, 68, January issue, 1951), I ventured to comment more extensively on the book as a whole and specifically on the section dealing with communities. The present review will deal only with the last section, entitled "Ecology and Evolution" and written by A. E. Emerson.

This section, 132 pages in length and a book in itself, is divided into five parts: ecology and genetic variation, ecology and isolation, adaptation, natural selection, and evolution of interspecies integration. The part on natural selection is the longest and its subheadings are preadaptation and habitat selection, selection pressure, competition, adaptive radiation and convergent evolution, ecological position and homeostasis, regressive evolution, retardation of evolution, and organismic levels and selection. An earlier section, "Biotic Factors in Relation to Individuals" (pp. 227–262), written by Allee and Schmidt, serves in large part as a good introduction to the chapters on evolution. There is, however, a considerable overlap in treatment of parasitism and mutualism between the two sections.

Because none of the other major topics dealt with in this book has been so widely under discussion in the recent literature, the section on evolution is the most vulnerable to critical scrutiny. Its organization, while appropriate, suggests no important departure from earlier treatments of much the same material, except for the ecological emphasis. This applies to concepts and principles more than to examples, of which there are many unfamiliar and interesting ones. In fact, the absence of reference to certain concepts currently under discussion suggests that much of the material may have been at least organized if not written before the appearance of the last decade's bulky literature on evolution. Some examples of such concepts are panmixia, polytypic species, and evolutionary rates in general, not just retardation and regression as discussed by Emerson.

There are many comments, unavoidably rather assertive and therefore appropriately challenging, which will raise questions in the minds of readers; some important examples of this may be cited since a comprehensive critique of the work as a whole is almost out of the question.

Page 605: "Much nonadaptive evolution at the infraspecies and species level may take place through the action of isolating factors in the absence of selection." An analysis of this statement leaves one uncertain as to how strongly the author meant it, but let us take it literally, as most readers will, I believe, even though, in the preceding sentence, selection is said to be the primary factor in divergent evolution. Whether there can be *much* nonadaptive evolution seems now to be so big a question that this statement, divested of immediate reference to specific cases and cast free of certain other relevant matters, as it is in context, sounds important but says little. Later (page 608) the author admits difficulties in identification of cases illustrating non-adaptive divergence of populations isolated merely topographically. What is more important, there is a confusion here of non-adaptive divergence at the subspecies level and *supposedly* nonadaptive diverg-

[1] W. C. Allee, A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. Principles of animal ecology. W. B. Saunders Co., Philadelphia and London, 1949: i–xii, 1–837, figs. 1–263. $14.00.

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ence at the *species* level, in either case as a result of topographic isolation. This confusion results from the species criteria used by the author.

Page 609: "Land snails of the islands of the South Seas . . . evidently have a high mutation rate and low vagility, with the result that distinctive populations may be recognized in valley woodlands separated by treeless ridges." Is a high mutation rate necessarily a part of this picture?

Page 622: "Mutations affecting the protein composition of the semen could well initiate the division of a species [in *Drosophila*]." This possibility seems very unlikely since any mutant would be eliminated because of reproductive ineffectiveness. The interspecific insemination reactions observed in crosses of *Drosophila* can be regarded as merely secondary accompaniments of more basic divergences, under polygenic control, which is stressed by Emerson in another connection (page 616).

Page 624: Hybrid elimination and hybrid origin of species is overstressed by Emerson because of his loose species concept. The discussion of hybrid relations includes no mention of the basic distinctions made by Mayr between primary and secondary contacts within polytypic species. Granting that hybrid elimination may isolate reproductively two species otherwise not completely separated, this is followed by the statement that "Subspecies of Nevada mammals seem to illustrate selective hybrid elimination." This leaves one in doubt as to what is under discussion, genuine interspecific hybrids or mere intergrades. In the famous case of hybridization between the two warblers, *Vermivora chrysoptera* and *V. pinus*, I wonder if failure of the effects of hybridization to spread (judging by morphological characters, of course) is due not to hybrid elimination, but to infrequency of crosses and probable low relative survival in these migrating species.

Page 634: It has been proposed by Simpson that the best criterion for adaptation is an increase in numbers of a "better adapted group" in comparison with a "worse-adapted" group. This view is questioned by the author, and in the ensuing discussion, he stresses typical differences in population densities of animals in different trophic levels of the Eltonian pyramid; that is to say, predators are fewer than their prey. This is offered in refutation of Simpson's point, but is actually irrelevant, since Simpson's point, if it is valid, refers to differences in population densities of species with closely similar ecologic requirements or at least overlapping requirements and therefore to species in one trophic level. Simpson's comparison is a horizontal one, whereas Emerson questioned it on the assumption that it was a vertical one.

Page 657: It is suggested that the floristic diversity and sparse species populations of tropical forests is related to the mildess of the tropical climate, as constrasted with the situation in temperate regions. By diversity, we take it, is meant species enrichment of a given major community. Earlier (page 600), it is indicated that "more isolating factors and more ecological niches" in tropical areas explain satisfactorily the great diversity of species. These are all relevant points, of course; but here, as in other recent discussions of the same matter, the factor of community age is overlooked. Given two temperate region forests, one developed since the last glaciation and one whose history has been continuous through much of the Tertiary (e.g., deciduous forest of the southern Appalachians), and considering the history of adjacent areas, the latter can be expected to be and is more diversified. It follows that in continental tropical areas, centrally placed, where forests have had a varied, long, and continuous history, including migration and repeated isolation and reconnection, age under these circumstances promotes diversity, whatever else does.

Current discussion of isolating factors proceeds at such a clip that the reader not too familiar with the literature may be misled on several important points. Emerson takes exception to Mayr's argument concerning the indispensable role of a geographic (or spatial) break between allopatric forms before these become sympatric (see latest phrasing of the problem by Pittendrigh, Evol., **4**, 1950: 73–77). The impression is left (see particularly page 616) that Mayr describes the process of speciation as merely one of spatial separation of two forms which, when and if they meet, react as species. (This is an oversimplification even of the position he took in 1942, in his book.) But in fact, many of the points concerning habitat factors which Emerson sets forth as reservations would be granted by Mayr (see Evol., **1**, 1947: 266, 285). Recently Mayr (Evol., **2**, 1948: 375–376), by way of emphasizing that subspecific variation in plants and animals is of comparable adaptive significance, implies that such divergence is a typical preliminary to sympatry; whereas Emerson, interestingly enough, is inclined at certain points to minimize the adaptive significance of racial variation (see page 626, top of column 2; page 629, bottom of column 1).

But these differences in viewpoints are part of a larger problem, which is the species definition. The thought recurs to me that a systematist's working definition of a species may reflect the present state of affairs in the taxonomic history of his own special group. Emerson's definition of a species—an evolved or evolving, reproductively isolated, genetically dis-

tinct, natural population—allows for the recognition as species of any forms which are closely related, yet distinguishable, and which replace each other geographically but are topographically isolated. For by "reproductively isolated" he refers to any factor, extrinsic or intrinsic (see pages 605, 606, 626). As a student of termites, and perhaps among entomologists generally, Emerson may be right at home when he says (page 626), "Reproductive isolation, regardless of what factor keeps the genes from moving across the species boundary, is the more inclusive and practical characteristic of the majority of recognizable species." But among many students of higher vertebrates, this statement is simply unacceptable.

This much would hardly be worth saying were it not for the added point that differences between evolutionists in viewpoints as to the relative role of different isolating factors are, in significant degree I believe, related subtly to differences in the species definitions they use. Whether or not any backtracking is to be done from the strong position taken by Mayr, the fact remains that his emphasis of geographic isolation, with later and full recognition of the simultaneous significance of adaptive intraspecific variation, has provided a griphold previously lacking in the wide and confused array of evidence on isolating factors. And Emerson's discussion of isolating factors struck me as lacking direction. I think that when many systematists, entomologists and others, stop recognizing many allopatric forms as distinct species and when more patterns of geographic distribution are analyzed in terms of a more inclusive species concept, there will be a significant reconsideration of views beyond but quite contingent upon the species concept. This is said more in anticipation than criticism, since insects and other invertebrates provide such superb material for the study of many speciation problems.

Some of a reader's difficulties in coping with these matters may result from an indecisive handling of the terms allopatric and sympatric, over and above their inherent difficulties. Thus, on page 612, reference is made to interbreeding open-stream and cave-dwelling populations of a fish forming an ecocline (discussed more fully on page 674). The two populations, whose morphological characters change along a continuous gradient, are placed in separate genera by ichthyologists, but Emerson calls them ecological subspecies. Then follows a startling statement: "Some authors would classify these as allopatric; we call them sympatric. Such difference of opinion revolves around the definition of categories." There is evidently no error here, for on page 616, one reads, "The line of division between sympatric and allopatric distributions of closely related species is arbitrary in a great many instances." Is not allopatry or sympatry a matter of demonstrable fact according to the case under study? Either two species are segregated spatially or they are not, whichever the available information indicates. The exceptions are probably not as numerous as Emerson's statements imply. How the two populations of fish, intergrading along a gradient, can be regarded as sympatric, especially after Emerson himself calls them subspecies, is difficult to understand.

For readability, I found the section on evolution more variable than any other part of the book. This may derive in part from variation in the author's own enthusiasm about certain topics and from changes which manuscript in so large an undertaking as this suffers in the course of publication. At least once the author seems to have overworked his cautiousness; *viz.*, "Many intraspecies populations evolve as units" (page 698). At least to the extent that evolution is a population phenomenon, do not *all* intraspecies populations evolve as units?

The foregoing discussion will, I hope, recommend Emerson's work as an important source of many thought-provoking ideas. It is also important for other reasons. The chapters on adaptation and natural selection are especially valuable syntheses of a wide array of factual information, and I found them especially stimulating. The chapter on interspecies integration and the ecosystem presents fully and well the author's support for the concept of the supraorganism. Regarding the latter, which has received so much varied comment, it seems worthwhile to quote one of Emerson's statements (page 694): "Even the social insect supraorganism is more soundly analogized with a primitive multicellular organism such as a sponge, than with a highly complex coordinated vertebrate organism." On this basis the concept of the supraorganism would appear to be an instructive one, and I thought it was used with more discretion in the chapters on evolution than elsewhere in the book. Also in the terminal chapter there is a good review of the role of biotic barriers in the structure and evolution of communities, well worth the careful study of students of habitat selection.

In having made so comprehensive a treatment of evolution a part of a book on general ecology, Emerson has taken care of a critical need in the current literature. Only those aspects of evolution having ecological relevance are discussed at length. Without a geneticist's background, I cannot judge whether the resulting presentation is too one-sided, but my impression is that it is not. Rather, this book confirms the trend indicated by other authors, that further elucidation of various fundaments of evolutionary theory must come from studies more or less strictly ecological. This book effectively reinforces the

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view that laboratory-explored genetical mechanisms, however important and relevant to evolutionary theory, do not in themselves answer conclusively the increasingly frequent questions about evolutionary dynamics.

By way of organization, the section on evolution, as a part of a book on ecology, might have been more unified if it had been consistently guided by some basic theme as the pyramid of numbers and the evolutionary consequences of fundamental differences between the several trophic levels. Such an attempt may now seem premature, yet this very theme is suggested in an earlier section, "Biotic Factors in Relation to Individuals" (see above), and in a recent book by Schmalhausen (Factors of evolution, 1949). Perhaps in setting the scene for that synthesis, Emerson's broad treatment of evolution and ecology has done its greatest service.

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EARTH RHYTHMS AND EVOLUTION [1]

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Professor Umbgrove has an original approach to his subject; he sees earth history on a very large scale and his discussions range from the astronomical origin of the earth through earth structure to the evolution of life. In "The pulse of the earth" he considered such topics as space and time, mountains, basins, oscillations of the crust of the earth, island arcs and the rhythm of life. Evolution includes not only organic evolution, but the development through time of the earth and of the physical environments in which life has progressed.

His new book, "Symphony of the earth," is perhaps not as coherent a whole as "The pulse of the earth," since it consists primarily of several lectures and discussions that have been presented at different times and places during the past few years. Yet the thread of a dominant idea ties these contributions together; it is the thought that thoughout earth history there has been a long rhythm of events, a rhythm that is reflected by such broadly different natural phenomena as the rotation of the galaxy, mountain building, the evolution of climates, the formation of basins and domes, and the differentiation of land plants. The rhythm, Professor Umbgrove thinks, is a cycle of about 250 million years, and its climaxes are represented at the beginning of the Cambrian period, during the closing phases of the Paleozoic Era and at the present time, at which three points in time there are maxima of the various phenomena mentioned above. Such a rhythm, it is held, has had a profound influence on the evolution of life.

To students of evolution the final chapter of the book, "Life and its Evolution," is of particular interest. Here there is presented a broad résumé of organic evolution, with particular emphasis given to some of the principles of evolution as revealed by the fossil record. There are discussions of the differentiation of natural populations to form species, of growth and form, of tempo in evolution, of adaptive radiation, of convergence and parallelism and of the problem of orthogenesis. Professor Umbgrove is impressed by the apparent orthogenetic aspect of many evolutionary lines seen in the fossil record, although he is careful to indicate that orthogenesis is not rectilinear evolution, as it has so often been interpreted.

He then goes on to a discussion of what he considers the three groups of theories that have attempted to explain the evolution of life, namely the group of vitalistic theories, that of the materialistic theories and finally the concept of holism. From his survey of such interpretations, Umbgrove finds that none of the theories is completely satisfactory as an attempted explanation of evolution.

Therefore he turns to the concept of complementarity, as he states it in this chapter. He feels that the living system is bound up with material processes, with which it forms a whole. Again we come to the broad view of the world and life that characterizes Umbgrove's thinking. Yet even complementarity fails to explain fully the interrelationships between life and the physical universe. "The farther science tries to penetrate into the secrets of the universe, the less is human imagination able to grasp the results attained." This attempt to consider life and the physical universe as a whole becomes so staggeringly complex that it is beyond the comprehension of a single mind.

However, the universe and its life does form a harmonious entity. And some of the evidence of this is in the rhythm of the earth that Umbgrove elucidates in this and in his previous works.

[1] J. H. F. Umbgrove. 1950. Symphony of the earth. Martinus Nijhoff, The Hague, xii + 220 pp.

COMMENTS ON EVOLUTIONARY LITERATURE*

ERNST MAYR

Hominid evolution.[1] In this well-balanced survey of new discoveries in East and South Africa, Le Gros Clark makes several important points. Not only was the separation of anthropoids from the cercopithecoids completed by early Miocene times, but the anthropoids themselves had already divided into several branches, of which the *Pliopithecus* group (with *Limnopithecus*) is clearly related to the gibbons. None of the Miocene forms apparently had the brachiating specializations of the modern anthropoids. Three species of *Proconsul* are of special significance since they combine primitive cercopithecoid features with those of the pongid African apes. "They appear to have been active, running and leaping creatures adapted for a quadrupedal type of locomotion like the modern cercopithecoid monkeys . . . and were certainly not adapted for a brachiating mode of life." In view of the recent interpretation of the evolution of canines and premolars in the prehuman primates, there is no longer any objection to a morphological series leading from "*Proconsul* to the various genera of the Dryopithecinae, and from a progressive dryopithecine type such as *Ramapithecus* to the precursors" of modern man. In a discussion of the South African Australopithecines Le Gros Clark stresses their human characteristics, which indicate that they were not far from the main line of human evolution, if not actually part of it. Also important is the fact that the various forms are rather similar in their essential characteristics (notwithstanding the several different generic names they have received from their enthusiastic discoverer, Robert Broom).

Natural selection in man.[2] The new volume on the problems of race formation in man is a refreshing reaction against the trend in the recent anthropological literature to ignore or even to deny the role of natural selection in the formation of human races. The authors show how many physical and racial characteristics, such as general stature, subcutaneous fat, hair form, etc., give indications of correlation with the environment. The most important conclusion of modern racial studies is, of course, that all races are highly variable, even the "purest" ones. Nowhere has the typological approach created greater havoc than in the study of human races. Recent work on balanced polymorphism indicates that the variability is not due merely to mixture, mutation, or random fixation in small populations. Rather it appears probable that in many of these variable loci as, for instance, those controlling blood groups and constitutional types, the heterozygotes may have superior viability. The very pronounced trends in human evolution toward thinner skulls, smaller jaws and teeth, rounder heads, and many other characteristics also indicate selection. The difficulties in this field are enormous. The fact that such unlike peoples as the Congo Pygmies, Hindus, and Mongols show a similarity in their blood group genes (high incidence of B) has been quoted as indication of lacking adaptive significance of this gene. Actually, of course, the adaptive value of a gene may depend to a large extent on the genetic background in which it is placed, and similar gene frequencies in such different environments as central Asia, India, and the Congo forest do not disprove a selective value of the respective genes. Little as we know about the adaptive significance of physical characters in man, we know even less, in fact virtually nothing, about non-physical characters. However, it is obvious from twin studies that at least some of them have partially a genetic basis and are thus exposed to selection. The study of man still has a long way to go.

Lava reptiles.[3] Mammals and terrestrial birds in desert regions are often cryptically colored, blackish on lava, whitish on white sand. Several subspecies of pale lizards are known from the White Sands of New Mexico. In six spe-

* At the 1950 Annual Meeting it was voted to have a short survey of the current evolutionary literature as a regular feature of EVOLUTION. This literature is still badly scattered and remains largely unknown to members of the Society with poor library facilities. The Editor asked me to organize such a survey section and Drs. Harlan Lewis (botany) and Bobb Schaeffer (paleontology) have kindly agreed to serve as contributors in subsequent issues. There is no intention to provide in this section a full review and abstract of the evolutionary literature. The contributors will discuss only such papers as come to their attention and as appear especially interesting. The present installment deals with papers that have recently reached the reviewer's desk.

[1] W. E. Le Gros Clark. 1950. New paleontological evidence bearing on the evolution of the Hominoidea. Quart. Jour. Geol. Soc. London, **105**: 225–264.

[2] C. S. Coon, S. M. Garn, and J. B. Birdsell. 1950. Races—A study of the problems of race formation in man. Charles C. Thomas, Springfield, xiv + 153 pp.

[3] T. H. Lewis. 1949. Dark coloration in the reptiles of the Tularosa Malpais, New Mexico. Copeia: 181–184.

cies of lizards and snakes from the black Tularosa Malpais (lava) specimens of four appeared distinctly darker than material from the adjacent desert. The samples were, however, very small.

Adaptive speciation.[4] It is widely known that the Hawaiian honeycreepers are an even more spectacular illustration of adaptive radiation than Darwin's finches on the Galapagos. Amadon has now produced a companion volume to Lack's work on Darwin's finches. A whole rich family evolved from a tanager- or coerebid-like ancestor. Now there are 2 subfamilies, 9 genera, and 22 species with 39 subspecies. As in most rapidly evolving bird groups, the bill is the most plastic character, varying from that of a grosbeak to a sickle-bill. As in Darwin's finches this invasion of new ecological niches is correlated with geographical speciation, even though in the end as many as 15 species may be found on a single island (Hawaii). Although not a single fossil is known, distribution patterns and the appearance of many intermediate forms permit a rather detailed reconstruction of the evolutionary paths leading to the present diversity. The great rôle played by competition is pointed out for many specific examples. Unfortunately at least 8 of the 22 species became extinct during the past 100 years and only 2 species remain common. This is a most revealing analysis of a spectacular story of evolution, a story which has often been very differently interpreted in the past.

Evolution in myrmecophilous beetles.[5] The paussids are a group of beetles which have become adapted to living with ants. They evolved from the tribe Ozaenini of the Carabidae. This evolution began when a primitive carabid beetle entered an ant's nest somewhere in the tropics of Asia or Africa, perhaps seventy or eighty million years ago. Darlington shows how its descendants became better and better adapted to life with ants and how evolution proceeded (often in a parallel manner) through the development of new organs (e.g., trichomes) and loss of old ones. Genitalic armatures usually evolve rapidly in insects. In these paussids they are conservative in comparison with those external structures that are directly involved in the myrmecophilous habits and thus most strongly exposed to selection pressure. These structures evolved almost "explosively" in the derivative paussids since the time of the Baltic amber (Oligocene). Paussids are not found in the nests of the more primitive ants (e.g., Ponerinae and Dorylinae), which confirms their rather recent origin. Many of the annectant forms with the Ozaenine carabids are still in existence, which facilitates the study of the evolution of this fascinating group.

There is another recent review of the family[6] with a general survey of the ecology, zoogeography, and taxonomy of the group, and a list of the 281 African species. Most of these (210) belong to the genus *Paussus* with its highly specialized antennae. Paussids produce a secretion which is very attractive to ants. Species of ants which feed on aphid "honey" have no paussid guests.

Competition in a specialized niche.[7] No less than 51 species of nematodes have been found in cow dung on European pastures. For 22 it is the exclusive habitat, for 10 it is a typical habitat, for the remaining 19 species it is only an occasional habitat. Dung beetles carry the nematodes to new sources of food and large numbers of nematodes are sometimes found on a single beetle. The various species of nematodes feed apparently not on the dung itself but on specific bacteria, fungi, and other microorganisms. As the succession of this microflora changes with the aging of the dung, so does the nematode fauna. In addition, there is a specialization into "surface" species and "interior" species. The nematodes in turn are the chief food of various insect larvae in the dung. Thus it seems that even a lowly piece of cow dung can serve as material for a fascinating ecological-evolutionary study.

Ecological niches in tropical Drosophila.[8] One *Drosophila* species looks to a non-specialist very much like any other. Feeding on fermenting fruit—as they are popularly supposed to—one might not expect more than a few species at any one place according to Gause's rule. That this is not so has been shown particularly by Patterson and his co-workers who found more than 50 species in Texas alone. Dobzhansky's work indicates that the number of species to be found at a given place in tropical Brazil may be twice as high. In spite of their morphological similarity each of these species occupies a somewhat different niche. It will take a long time before we know all these niches, since we know next to nothing even about the niches occupied by our temperate zone species. There

[4] D. Amadon. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist., **95**: 151–262, figs. 1–23, plates 9–15. $1.75.

[5] P. J. Darlington, Jr. 1950. Paussid beetles. Trans. Amer. Ent. Soc., **76**: 47–142.

[6] A. Reichensperger. 1948. Die Paussiden Afrikas. Abh. Senckenb. Naturf. Ges., **479**: 1–32.

[7] H. Sachs. 1950. Die Nematodenfauna der Rinderexkremente. Zool. Jahrb. (Syst.), **79**: 209–272.

[8] T. Dobzhansky and C. Pavan. 1950. Local and seasonal variations in relative frequencies of species of *Drosophila* in Brazil. Jour. Animal Ecol., **19**: 1–14.

are indications that the larval stage is the crucial competitive period. Some species are very specialized, some are more tolerant ecologically, sometimes helped by genetic polymorphism. The authors find changes of relative frequencies of the different species from month to month even in a region with a relatively uniform superhumid tropical climate. The dynamic balance of the various species is shifting continuously. The amount of ecological divergence within the morphologically uniform genus *Drosophila* is of great evolutionary interest.

Species recognition in fishes.[9] Readiness for mating in animals is induced by adequate stimuli from the sex partner. If this potential mate belongs to an alien species the stimuli are usually insufficient for mating. An increasing number of students has been studying the nature of these stimuli. In the closely related species of African Cichlids, *Tilapia heudeloti* and *T. natalensis*, the males display indiscriminately to females of either species, exactly as in some closely related species of *Drosophila*. However, females are usually stimulated only by males of their own species. Since the movements in the courtship display are identical in the two species, it may be the coloration of the courting male which serves as isolating mechanism.

Geographic variation of sterility factors.[10] Hybrids produced by crossing individuals from five different local populations (each in a different stream) of the fish *Cobitis taenia striata* in western Honshu (Japan) were sterile. In a few cases there was partial fertility. This is reported to be the first case of sterility between geographical races of a species of fish.

Evolution in game animals.[11] More is known about the composition of populations in game animals than almost any other kinds of animals. It is most praiseworthy that Voipio attempts to interpret in terms of modern population genetics the extensive material available on Finnish game species. These data are based on annual censuses covering many decades. Among results of special interest are these: there is much geographical variability in all these species, a variability affecting not only size and other morphological characters but also many physiological and ecological traits, with the result that each local population is (through selection) adapted for its particular locality. Transplanting local stocks into new localities usually leads to disastrous losses. Author gives many interesting data on the frequency of polymorph genes in Finnish fur bearers and trends in the fluctuation of these genes (squirrel, fox, arctic fox, and muskrat). He proposes certain management procedures by which the frequency of the most desirable of these genes (e.g., silver fox, black muskrat, palmate moose) could be increased in populations, based on the correct assumption that most of these genes have a selective significance. The rôle of the heterozygotes, presumably important in much of this balanced polymorphism, is ignored. The game management literature is a hardly touched gold mine of information for the student of the dynamics of wild populations. Game populations are even amenable to much experimentation. Voipio's paper suggests that collaboration between population geneticists and students of game management would be of mutual benefit.

Geographical and temporal variation in polymorphism.[12] There already is extensive literature on the polymorphism of *Harmonia axyridis*. The authors give precise data on the geographical variation in the frequency of the various alleles in Japan. There are fairly regular clines in the frequency of some of the patterns, apparently closely correlated with climate, particularly humidity, as previously pointed out by Dobzhansky. Samples taken at intervals of 15 to 30 years are available for several localities. At some places there has been hardly any change in 30 years, at others some patterns decreased significantly. In Sapporo, for instance, the *succinea* type dropped from 84 per cent in 1923 to 43 per cent in 1944. The genes are considered neutral and consequently no serious effort is made to correlate these genetic changes with possible changes of climate or other factors of the environment.

Adaptive polymorphism.[13] A white color phase occurs in females of several species of the pierid butterfly genus *Colias*. There is a tendency for this gene to reach its highest frequency in the northwest (Alaska, Yukon) and its lowest in the prairie region of southern Alberta and Saskatchewan. This is illustrated in a series of 6 maps and 6 tabulations of sample frequencies. It is not yet known what the physiological superiority of the heterozygotes

[9] A. Seitz. 1948. Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae). Z. f. Tierpsychologie, **6**: 202–235.

[10] S. Minamori. 1950. Jour. Sci. Hiroshima Univ., (B), **11**: 55–59.

[11] P. Voipio. 1950. Evolution at the population level with special reference to game animals and practical game management. Papers on Game Research, **5**: 1–176, Helsinki.

[12] T. Komai, M. Chino, and Y. Hosino. 1950. Contributions to the evolutionary genetics of the lady-beetle, *Harmonia* I. Geographic and temporal variations in the relative frequencies of the elytral pattern types and in the frequency of elytral ridge. Genetics, **35**: 589–601.

[13] W. Hovanitz. 1950. Parallel geographical variation of dimorphic color phases in North American species [of *Colias*]. Wasmann Jour. Biol., **8**: 197–219.

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may be, which is obviously the cause of this geographically variable balanced polymorphism.

Variation in a domestic species.[14] The known variations in the color pattern of domestic pigeons are compared with those of 277 wild species of the family Columbidae. It is found that each subdivision of the pigeon family has a number of characteristic color patterns. The variation in color pattern found among domestic pigeons consists primarily of irregularities and other aberrations, but does not reveal any evident parallelism with color patterns found in other genera of pigeons.

A French survey of the new systematics.[15] The well-known French herpetologist Laurent gives here a succinct, well-balanced discussion of the modern concepts of species and race and of the effect of the new concepts on systematics and evolutionary studies.

Polytypic species in ants.[16] The nomenclature of ants has formerly been the despair of non-specialists (and presumably the specialists as well!). Quadrinomials and quinquenomials were quite customary, and there was an implication that the species structure of ants was quite different from that of other insects. Creighton's monograph clears this up in a manner that is as convincing as it is satisfactory. Species of ants are like those of other bisexual animals, and the geographical race or subspecies is the only infraspecific category worthy of recognition. There are many complexes of exceedingly similar sibling species which are still insufficiently analyzed (e.g., *Formica fusca* group) and which present fascinating evolutionary and ecological problems. It is to be hoped that more workers undertake studies like those of Gösswald on the European species of the *Formica rufa* group.

Speciation in ancient lakes.[17] The phenomenon of species flocks in lakes has stimulated much speculation as to possible speciation mechanisms. "Explosive" or "ecological" sympatric speciation was postulated by several authors. In this thorough review Brooks presents a wealth of detailed facts concerning these species flocks in Baikal, East African lakes, Titicaca, Lanao, and others. He shows that, as in terrestrial animals, spatial isolation must be held responsible for the origin of these flocks. The details can be reconstructed fairly satisfactorily for the gammarids of Lake Baikal because their present distribution is rather well known. Subdivision of the lake into large basins with subsequent amalgamation has played a large rôle. A long coast line on which ecologically suitable areas are separated by long unsuitable stretches is an additional important speciation factor in Baikal, Tanganyika, and Nyasa. In shallow Victoria Nyanza much speciation took place apparently in small peripheral lakes that were subsequently reincorporated in the main lake. Every student of evolution should study this illuminating review which has brought order into the previously chaotic subject of lake speciation.

Circular overlap.[18] The Greater Titmouse (*Parus major*) was one of the first described cases of circular overlap. The ends of a circle of races around the central Asiatic highlands meet in eastern Asia on the Amur River without interbreeding. This recent study shows that matters are a little more complicated than thought at first. The authors show in a most instructive map that the 33 recognizable subspecies actually fall into four subspecies groups. The European group (yellow and green) interbreeds with the gray Indian group in northern Persia, and the Indian group with the green-backed east Asiatic group in south China. In addition, there is a group of gray and very long-tailed subspecies in Turkestan which seems to come into contact with the other forms in Transcapia and the Altai without showing signs of interbreeding (see Vaurie, C. 1950. Amer. Mus. Novitates, no. 1459 for details). Finally, there is the very similar *P. monticola* which from the Himalayas to south China acts in most places (not always!) like an altitudinal representative of *P. major*. A most interesting case of active speciation.

Hybrid swarms in birds.[19] The two species of red-eyed towhees in Mexico, *Pipilo erythrophthalmus* and *P. ocai*, coexist as good species of Oaxaca. Not one of 64 available specimens shows the slightest trace of hybridization. Three of the 5 subspecies of *ocai* and 5 of the 10 Mexican subspecies of *erythrophthalmus* are "pure." The others participate to a lesser or greater extent in hybridization between the two species. On Mount Orizaba (Est. Puebla) the two species are well defined, but among 109

[14] M. v. Mikulicz-Radecki. 1950. Studien über Musterung und Färbung von Wild- und Haustauben. Zool. Jahrb. (Physiol.), **62**: 211–354.

[15] R. Laurent. 1948. Problèmes taxonomiques. L'espèce et la race. La phylogenèse et la systématique. Ann. Soc. Roy. Zool. Belg., **78** (1947): 56–101.

[16] W. S. Creighton. 1950. The ants of North America. Bull. Mus. Comp. Zoöl., **104**: 1–585, 57 plates.

[17] J. L. Brooks. 1950. Speciation in ancient lakes. Quart. Rev. Biol., **25**: 30–60, 131–176.

[18] J. Delacour and C. Vaurie. 1950. Les mésanges charbonnières (révision de l'éspèce *Parus major*). L'Oiseau, **20**: 91–121.

[19] C. G. Sibley. 1950. Species formation in the red-eyed towhees of Mexico. Univ. California Publ. Zool., **50**: 109–194, plates, 11–16, 18 figs.

collected specimens 13 show evidence of hybridization, 6 being predominantly *erythrophthalmus* and 7 predominantly *ocai*. On an isolated mountain in the state of Jalisco (Cerro Viejo) a population is found which appears to consist exclusively of hybrids. No two of 76 collected specimens are alike and all of them show traces of hybridism, with the majority of the birds about intermediate between the two species (similar populations have since been discovered on other peaks). Finally, there is a series of variable populations across the Mexican plateau between the Sierra Madre Occidental and the Sierra Madre Oriental in which each population is somewhat intermediate between its neighbors east and west, thus completely bridging the gap between the two species. If a hybrid index is calculated with "pure" *ocai* as 0 and "pure" *erythrophthalmus* (*orientalis*) as 24, the following figures are obtained on a west-east transect: Jalisco 1; Tancitaro (etc.), Michoacan 4; Patzcuaro, Michoacan 7.8; Mil Cumbres, Michoacan 13.5; Michoacan-Mexico border 15.8; west side of the Valley of Mexico 16.9; Mt. Popocatepetl 19.8; southern Hidalgo 22.4; Sierra Madre Oriental 24. The populations with a hybrid index of less than 12 are classified with *ocai*, the others with *erythrophthalmus*.

Sibley has thus found a highly interesting situation (somewhat like that described by Chapin for *Terpsiphone*) that the two species act like perfectly good species in parts of the range, sparingly hybridize in parts, and completely in others. Much as they will be deplored by the orderly taxonomist, such cases shed light on the origin of isolating mechanisms. Sibley shows how the many points of hybridization might be explained by a single primary event of hybridization and subsequent introgression, and thus a weakening of the isolating mechanisms. We must be particularly grateful to the author for his painstaking and illuminating analysis in view of the rarity of introgression among the higher vertebrates. The paper is illustrated by two beautiful colored plates and many maps and diagrams.

Natural selection.[20] Besides its intrinsic interest to students of human populations, Muller's discussion is particularly valuable for bringing out the effects of slightly dominant deleterious genes, as well as the cumulative effects of such genes. It should be read by all those who believe that a gene with slight effect is inconsequential.

[20] H. J. Muller. 1950. Our load of mutations. Am. Jour. Human Gen., **2**: 111–176.